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Towards Regional Benchmarks of Fish Productivity in Nearshore Marine Ecosystems: Model Framework, Habitat Comparisons, and Examination of Regional Data

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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TABLE OF CONTENTS

ABSTRACT V

RÉSUMÉ VI

INTRODUCTION 1

METHODS 3

- MODEL STRUCTURE 3
- CALCULATION OF FISH PRODUCTION METRICS USING MODEL OUTPUT 5
- SENSITIVITY ANALYSIS 5
- UNCERTAINTY QUANTIFICATION 6
- MODEL APPLICATION 7
  - Eelgrass Beds and Adjacent Bare Habitat: Field Site Description 7
  - Eelgrass Beds and Adjacent Bare Habitat: Fish Sampling 7
  - Rockweed Beds and Interspersed Bare Habitat: Field Site Description 8
  - Rockweed Beds and Interspersed Bare Habitat: Fish Sampling 8
  - Fish Age, Density, Data Calibrations, and Final Data for Model Input 8
  - Fish Density Estimates, Gear Capture Efficiency, and Visual Detection Probability 9
- COMPARISONS OF HABITAT SPECIFIC ESTIMATES OF PRODUCTION 9
- PRELIMINARY REVIEW OF REGIONAL FISH DATA FOR MARITIMES CANADA 10

RESULTS 10

- FIELD DATA USED FOR MODEL APPLICATION 10
- MODEL ESTIMATES OF PRODUCTION POTENTIAL, EQUIVALENT ADULTS, AND AREA PER RECRUIT 11
- INCREASED PRODUCTION POTENTIAL IN EELGRASS OR ROCKWEED RELATIVE TO BARE HABITAT 12
- MODEL SENSITIVITY AND UNCERTAINTY QUANTIFICATION 12
- REVIEW OF REGIONAL NEARSHORE FISH DATA 13
  - Dataset 1: Skinner and Courtenay (Skinner 2013) 13
  - Dataset 2: Locke and Bernier 13
  - Dataset 3: CAMP (Community Aquatic Monitoring Program), M.-H. Thériault, S. Courtenay, M. Boudreau (Weldon et al. 2005, Weldon et al. 2009, DFO 2011) 14
  - Comparison of field density of fishes captured across all studies 15

DISCUSSION 15

- MODEL FRAMEWORK TO DETERMINE FISH PRODUCTIVITY 15
- METRICS OF FISH PRODUCTIVITY 16
- HABITAT UNITS OF NEARSHORE FISH PRODUCTIVITY 16
- REGIONAL BENCHMARKS FROM AVAILABLE NEARSHORE FISH DATA 17
- SUMMARY 18

ACKNOWLEDGEMENTS 18

REFERENCES CITED 18

TABLES 22
FIGURES 30
APPENDICES 43
APPENDIX A 43
APPENDIX B 44

ABSTRACT

Regional benchmarks of fisheries productivity could guide decision making by the Fisheries Protection Program (FPP) for authorization, compensation, and offsetting of serious harm. In particular, benchmarks are needed for nearshore marine habitats, which are important for fisheries production. Here we present a model framework to estimate fish production for the data and information poor situations generally found in nearshore ecosystems. We also review available fish data for nearshore habitats in Maritimes Canada and comment on the potential for using these data to develop regional benchmarks.

Our model framework estimates fish production using an age-structured Leslie population matrix and is formulated with length-dependent survival and fecundity, coupled with growth and length-weight functions. Uncertainty quantification is included and accounts for parameter dependence. We made the simplifying assumption of steady-state populations, scaling the resultant proportional stable age distribution with observed fish density (in at least one age class). Mortality and growth were estimated from regional values. Model outputs include species-specific abundance, biomass and production per age class across the entire lifespan of the fish. We apply the model using data from Eelgrass (*Zostera marina*) beds, Rockweed (*Ascophyllum nodosum*) beds, and associated bare habitat on the Atlantic coast of Nova Scotia, Canada. We present three different candidate metrics of fish production, including production potential, equivalent adults, and area per recruit. Fish production of most species was higher in Eelgrass or Rockweed relative to bare habitat. The model framework is general in that it can be adapted and extended as more comprehensive data sets become available, and thus has application beyond that presented here.

Additional datasets of fish assemblages in Eelgrass beds from the southern Gulf of St. Lawrence were examined for their potential in developing benchmarks. These data were of species-specific capture density, with typically no information on fish biomass or age class. Use of these data in our model to estimate production would require assumptions of age or size structure. Differing capture efficiencies of sampling gear would also need to be taken into account. Regardless, the compiled data can provide insight into various aspects of fish production across different spatial scales, including fish density, community structure, habitat associations, and temporal variability.

Vers des points de référence régionaux pour la productivité du poisson dans les écosystèmes côtiers : cadre modèle, comparaisons d'habitats et examen de données régionales

RÉSUMÉ

Les points de référence régionaux de la productivité des pêches pourraient orienter la prise de décisions dans le cadre du Programme de protection des pêches (PPP) aux fins d'autorisation et de compensation des dommages sérieux. En particulier, des points de référence sont nécessaires pour les habitats marins côtiers, qui sont importants pour la production des pêches. Dans le présent document, nous présentons un cadre modèle pour estimer la production de poissons dans les situations où les données et les renseignements sont limités, ce qui est généralement le cas pour les écosystèmes côtiers. Nous examinons également les données sur les poissons disponibles pour les habitats côtiers de la région des Maritimes au Canada et formulons des commentaires sur la possibilité d'utiliser ces données pour élaborer des points de référence régionaux.

Notre cadre modèle estime la production de poissons à l'aide d'un modèle matriciel de population de Leslie structuré selon l'âge dont la formule comprend la survie et la fécondité dépendant de la longueur, ainsi que les fonctions relatives à la croissance et à la relation longueur-poids. La quantification de l'incertitude est incluse et tient compte de la dépendance des paramètres. Nous avons émis l'hypothèse de simplification que les populations connaissent un état de stabilité, mettant à l'échelle la répartition selon l'âge stable proportionnelle en résultant avec la densité de poissons observée (dans au moins une classe d'âge). La mortalité et la croissance ont été estimées à partir des valeurs régionales. Les résultats du modèle comprennent l'abondance, la biomasse et la production par classe d'âge propres à l'espèce pendant toute la durée de vie du poisson. Nous appliquons le modèle en utilisant les données provenant des herbiers de zostère marine (Zostera marina), des herbiers de fucus (Ascophyllum nodosum), et de l'habitat nu associé sur la côte atlantique de la Nouvelle-Écosse, au Canada. Nous présentons trois différentes mesures proposées de la production du poisson : le potentiel de production, les équivalents adultes et la zone de recrutement. La production de poissons de la plupart des espèces était plus élevée dans l'habitat de la zostère ou du fucus que dans l'habitat nu. Le cadre modèle est général en ce sens qu'il peut être adapté et prolongé au fur et à mesure que des ensembles de données complets sont disponibles et a donc une application qui dépasse celle qui est présentée ici.

Des ensembles de données supplémentaires sur les assemblages de poissons dans les herbiers de zostère du sud du golfe du Saint-Laurent ont été examinés dans le cadre de l'élaboration des points de référence. Ces données concernaient la densité de capture propre aux espèces, en général sans renseignements sur la biomasse ou la classe d'âge des poissons. L'utilisation de ces données dans notre modèle pour l'estimation de la production nécessiterait des hypothèses quant à la structure d'âge ou de taille. La variabilité de l'efficacité de la capture et des engins d'échantillonnage devrait également être prise en compte. Quoi qu'il en soit, les données compilées peuvent donner un aperçu des divers aspects de la production du poisson à différentes échelles spatiales, y compris de la densité du poisson, de la structure des communautés, des associations d'habitats et de la variabilité temporelle.

INTRODUCTION

Canada's *Fisheries Act* was amended in 2012 to include Fisheries Protection Provisions that manage threats to the ongoing productivity of commercial, recreational, and aboriginal (CRA) fisheries. These provisions prohibit serious harm to the productivity of CRA fisheries, where serious harm is defined as "the death of fish, or the permanent alteration to, or destruction of, fish habitat". Proponents can apply for authorization if their project will cause serious harm. The Fisheries Protection Program (FPP) will consider (among other factors) contributions to fisheries productivity and the planned mitigation or offsetting of serious harm to determine if authorization is appropriate. Such decision making would benefit from representative estimates of fish productivity across broad spatial units.

Fisheries and Oceans Canada (DFO) Ecosystems Management has requested advice from DFO Science on regional benchmarks of fisheries productivity for marine ecosystems. Specifically, advice was requested on the feasibility of determining benchmarks, the relevant methodologies and appropriate spatial scales, and the applicability of the Area per Recruit (APR) metric. It is anticipated these benchmarks will be used for impact assessments in the absence of site-specific data, and to provide targets for and to evaluate outcomes of offsetting procedures for projects in marine ecosystems. The request for regional benchmarks illustrates the understanding that fish communities and associated productivity will likely differ among regions in Canada. Use of regional benchmarks instead of site-specific data provides an ecosystem approach that integrates aspects of productivity, biodiversity and habitat (Gavaris 2009). Regions can be delineated by geographic boundaries or by ecological characteristics based on climate, hydrology, geomorphic or chemical features, among others (de Kerckhove et al. 2017).

This request builds on a previous Canadian Science Advisory Secretariat (CSAS) meeting that evaluated regional benchmarks of fish productivity for freshwater ecosystems (DFO 2016). The meeting extended the original focus of habitat production (used for 'no net loss' of fish habitat) to fisheries productivity. The first research document evaluated regional differences in fish productivity in freshwater streams from relationships of biomass density vs. sample area and density vs. body size, as well as from data of species richness, biomass, and density evaluated across sites and years (Randall et al. 2017). It was determined that average biomass density of fishes was predictable among fisheries management areas. Regional benchmarks are feasible from available data, and fish productivity can be estimated from temperature regimes. A second research document provided a review of Ecologically Based Management Areas, and suggested that intermediate scale management areas (20,000 km^2) may be appropriate to delineate regional variation in aquatic metrics (de Kerckhove et al. 2017). Existing classification schemes and ecological models to predict freshwater fish production at different scales are available and relevant for regional benchmarks.

The science advice provided in the CSAS freshwater benchmark meeting is relevant to the current request for advice on marine fish productivity benchmarks. However, data on fish density, biomass, or productivity in nearshore marine ecosystems is sparse, despite the importance of nearshore habitats for nursery and feeding grounds for inshore and offshore fish (Jackson et al. 2001, Gillianders et al. 2003). Habitats with biogenic structure (e.g., Eelgrass (*Zostera marina*), Rockweed (*Ascophyllum nodosum*)) often exhibit higher fish abundance, biomass, and diversity relative to adjacent bare habitat (e.g., Heck et al. 1989), and in Atlantic Canada are used by several important CRA fishery species (e.g., White Hake, Cod, flounder, Pollock (Wong et al. 2016). Many different types of nearshore activities (i.e., dredging, infilling) may impact nearshore habitats and the fish communities that utilize these habitats. Thus, metrics of fish productivity in nearshore marine ecosystems, comparisons among habitat units,

and development of regional benchmarks would be particularly useful to guide decision making by FPP for these ecosystems.

Determining fish production in nearshore habitats is challenging given that data are often limited in their spatial and temporal extent. Most often, available data on fish abundance are from one or a few time points, and are rarely standardized to allow cross-study comparison or to account for gear selectivity. Data on body size or comprehensive time series of data required for fisheries models (i.e., recruitment, survival, growth, biomass) are generally not available. Here we develop a model framework to calculate fish production that can be used in the data poor situations generally encountered for nearshore ecosystem studies. This model framework has general application across species and ecosystems.

Our model framework uses a Leslie matrix from an age structured population model coupled with growth and length-weight functions. Specific strengths of the model are that it only requires minimal field data (density of fish in at least one age class) and estimates of survival and growth parameters from regional sources or the literature. We also provide uncertainty quantification for the model predictions. We apply our model framework to estimate the production of fish (i.e., fish and large decapods) derived from various nearshore habitats: Eelgrass (*Zostera marina*) beds, Rockweed beds (*Ascophyllum nodosum*), and associated bare habitat for the Atlantic coast of Nova Scotia, Canada.

We estimate species-specific fish production across the entire lifespan of the fish in the particular habitat of interest, regardless if the fish spends its entire lifespan in that habitat or not. This accounts for the fact that loss of fish from the habitat has population consequences beyond the loss of that fish biomass alone (Rago 1984, Boreman 1997). This also allows calculation of several different metrics of fish production that can account for habitat contribution to production in various ways. Here we present three metrics to illustrate the flexibility in the model estimates of production for construction of metrics useful for FPP. These metrics include:

i) production potential, defined as the total lifetime production of the fish (and similar to production foregone),

ii) adult equivalents, defined as the number of mature adults, and

iii) area per recruit, defined as the habitat area required to produce one mature adult.

These metrics are interrelated, and have been previously identified as potentially useful for FPP decision making (DFO 2015).

This work represents a first step towards the development of regional benchmarks of fisheries productivity in nearshore marine ecosystems for use by FPP. Specific objectives of this study were to:

1. present a model framework that can estimate lifetime fish production, appropriate for data limited situations, such as in nearshore ecosystems,
2. apply the model using field data of fish from Eelgrass, Rockweed, and associated bare habitats on the Atlantic coast of Nova Scotia,
3. compare three different metrics of fish production from model output that are relevant to FPP,
4. evaluate habitat-specific estimates of fish production, and
5. summarize and comment on the available regional nearshore fish data and its potential for developing regional benchmarks of fisheries productivity.

Note that our original motivation in developing a model framework to estimate fish production was to understand contributions by different nearshore habitats to ecosystem functioning, and to develop metrics of fish production relevant for habitat restoration and compensation activities (Wong and Dowd 2016). Our model was motivated by the types of field data available for nearshore ecosystems, typically estimates of density from various types of survey data, without comprehensive information of fish size, age-structure, or temporal trends. The model framework was designed to allow synthesis of these data, and also be extensible as further information was obtained. We primarily focussed on habitat-specific comparisons of fish production, and not on a regional assessment. Here, we extend our past work, and review new data, with the goal of assessing the potential for developing regional benchmarks for nearshore habitats.

METHODS

MODEL STRUCTURE

To determine species-specific lifetime fish production, we used a Leslie matrix from an age structured population model, coupled with length-weight relationships and the von Bertalanffy growth function.

The age-structured population model takes the form:

$$\mathbf{n}(t) = \mathbf{A}\,\mathbf{n}(t-1) \qquad (1)$$

where $\mathbf{n}(t)$ is a column vector whose elements contain the number of individuals (normalized per unit area, here m^{-2}) in each of the age classes at time t (here, a unit time increment is one year). The first element of $\mathbf{n}$ is age-0 abundance. The Leslie matrix $\mathbf{A}$ then provides for the annual change in numbers per age class from time $t-1$ to time t. It has the following form:

$$\mathbf{A} = \begin{bmatrix} f_0 & f_1 & f_2 & \cdots & f_{i-1} & f_i \\ s_0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & s_1 & 0 & \cdots & 0 & 0 \\ 0 & 0 & s_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & s_{i-1} & 0 \end{bmatrix}$$

where s_i and f_i are the survival and fecundity for age class i. Note that non-zero f_i in the first row will start at the age classes greater than or equal to the age at maturity, t_m. The size of the Leslie matrix $\mathbf{A}$ is set by the number of age classes to be included. Hence, given the age distribution at the initial time, $\mathbf{n}(0)$, the time evolution of the age distribution can be determined recursively using the difference Equation (1). For full details on age-structured population models, and Leslie matrices, see Caswell (2001).

For this study, only limited information was available. Typically, the field data were comprised of observed species-specific densities at certain ages (usually age class *0*) with little information on survival and fecundity. Hence, we made the simplifying assumption that the fish populations are in steady state (i.e., $\boldsymbol{n}$ is time invariant). This means that $\mathbf{A}$ can provide the proportional stable age distribution and there is no need to actually run the time-stepping model (Equation 1). Specifically, the steady state assumption requires that the leading eigenvalue of $\mathbf{A}$ is one (no population growth or decay). The proportional stable age distribution ($\mathbf{n}_{prop}$) is the associated dominant eigenvector (normalized to sum to one).

Implementation details are as follows. For each species, we included all age classes (based on known lifespan from the literature, t_{span}; Table 1; Wong and Dowd 2016) because lifetime

production comes not only from those age classes present (i.e., age-0 and juveniles that most often utilize nearshore habitats), but also from the production by absent adults (i.e., those in other habitats or offshore) derived from those younger present fish. Species-specific time to maturity was also taken from literature values (t_m; Table 1; Wong and Dowd 2016). Survival was calculated assuming a negative relationship between mortality and body size (Lorenzen 1996, Jung et al. 2009). Lorenzen (2000) found that the allometric relationship between natural mortality (m) and body length (L) is described by:

$$m_L = m_{ref}\left(\frac{L}{L_{ref}}\right)^c$$

where the subscript *ref* refers to the reference value and c is the allometric exponent. Lorenzen (2000) suggests that $c = -1$ provides the best performing model. We substitute this function into the survival relationship $s = e^{-m}$ to incorporate length dependent mortality as:

$$s_i = \exp\left\{-\left(\frac{m_{ref}L_{ref}}{\bar{L}}\right)\right\}$$

where $\bar{L} = \frac{1}{2}(L_i + L_{i+1})$. We use estimates of natural mortality (here, m_{ref}) derived from empirical relationships (Pauly 1980, Fishbase 2015, Wong and Dowd 2016) that include growth parameters and temperature, using a mean annual temperature of 8°C. We assume m_{ref} is defined at the median length L_{ref}. Note that fishing mortality is not included here because the purpose of this study is to estimate the production of fish from Eelgrass or Rockweed beds, irrespective of external pressures.

Little information was available on fecundity (f) for nearshore fishes, so we estimated its magnitude for each species by making use of the steady-state assumption. Note that the quantities t_{span}, t_m, and s define the Leslie matrix **A**, except for the values of the f. Fecundity was considered to be an allometric function of length, i.e. $f = f_{scale}L^{\beta}$ (Bagenal 1978; van der Lee and Koops 2015). Following these studies, we assumed $\beta = 3$, but estimated the scaling coefficient f_{scale}. This was done as follows. The steady-state assumption means that the leading eigenvalue of **A** must be equal to one, and hence, we choose the value for f_{scale} for which this condition holds. This is done by minimizing the cost function

$$J(f_{scale}) = \left(\lambda^*(f_{scale}) - 1\right)^2$$

with respect to f_{scale}. Here, $\lambda^*(f_{scale})$ is the leading eigenvalue of the Leslie matrix **A** constructed using a given value for f_{scale}. This univariate minimization of J is straightforward and robust (we used a golden search algorithm via the *optimize* function in R) and yields the requisite value for fecundity required for a steady-state population.

To determine the steady-state stable age distribution, we make use of field observations along with the computed proportional stable age distribution, $\mathbf{n}_{prop}$. For a given species, we generally have a density observation at some age class i, which we designate $n_{obs,i}$ (note that the consequences of observational uncertainty is taken up in uncertainty analysis below). The abundance distribution with age is given as $\mathbf{n} = \alpha\mathbf{n}_{prop}$ with the scaling factor $\alpha = n_{obs,i}/n_{prop,i}$ where $n_{prop,i}$ is the ith element of the vector $\mathbf{n}_{prop}$. (Note that in the relatively few cases where observations at multiple age classes were available for some species, the age distribution was fit to the observations with the scaling factor estimated via least-squares). The simplification of making a direct observation-based scaling of the proportional age distribution means that fecundity has no effect on the analysis (since its contribution is to age-class *0*, and the

observations serve to re-normalize the age distribution). However, we retain the more general formulation as it provides the basis for future studies with more comprehensive data sets.

These estimates of n_i were then used to determine fish production. First, length of an average individual at each age class i (L_i) was determined using the von Bertalanffy growth function (von Bertalanffy 1938):

$$L_i = L_\infty\left(1 - e^{-k(i-t_0)}\right)$$

where L_∞ is the asymptotic length, k is the growth coefficient (i.e., how fast a fish approaches L_∞), and t_0 is the age at zero length. L_i was converted to average individual weight at age class i (W_i) using the length-weight relationship (as reviewed by Froese 2006):

$$W_i = aL_i^b$$

where a and b are species-specific parameters. All growth and length-weight parameters were derived from the literature and databases, or from empirical relationships (Table 1; Wong and Dowd 2016). Production per age class (P_i) was then determined by $P_i = \bar{n}(W_{i+1} - W_i)$ where $\bar{n} = \frac{1}{2}(n_i + n_{i+1})$ and n_i is the density per age class as determined within **n** above (Chapman 1978).

CALCULATION OF FISH PRODUCTION METRICS USING MODEL OUTPUT

Model output consists of species-specific estimates (per m^2) of abundance, biomass, and production per age class for each habitat type. The output can be used in various forms to inform decision making for FPP. Here we present three potentially useful metrics based on previous DFO advice (DFO 2015):

1. Production Potential (PP): PP (here g wet weight m^{-2} y^{-1}) is the total lifetime production of the fish, regardless if it spends its entire lifespan in the target habitat. This accounts for the fact that destruction of fish in the habitat can have wide implications for the population beyond the loss of their biomass alone (Rago 1984, Boreman 1997). PP is similar to production foregone (scaled to per m^2 of habitat; DFO 2015). PP is calculated by summing across production per all age classes.
2. Equivalent Adult (EA): EA (here number m^{-2}) is the number of adults expected from the given number of fish observed in the target habitat. "Adults" are defined as reproductively mature fish, meaning age classes ≥ t_m in the Leslie matrix (DFO 2015). EA was calculated as the total number of adults across all mature age classes.
3. Area per Recruit (APR): APR (here m^2) is the area of the target habitat required to produce one adult recruit, with recruits defined as reproductively mature fish. APR was calculated as the inverse of the number of mature adults in the first recruiting age class produced per m^2 of habitat.

SENSITIVITY ANALYSIS

Sensitivity analysis of total abundance (n_{total}) and total production (production potential, PP) of each fish or large decapod species under variations in the model inputs was carried out. This included sensitivity of n_{total} and PP to variations in the inputs m_{ref}, t_{span}, t_m, and $n_{obs,i}$, as well as sensitivity of PP to variations in the inputs L_∞, t_0, k, a, and b. The following sensitivity metric was used:

$$S_{X,j} = \frac{1}{2\Delta}\left(\left|\frac{X(\theta + \Delta\theta_j) - X(\theta)}{X(\theta)}\right| + \left|\frac{X(\theta - \Delta\theta_j) - X(\theta)}{X(\theta)}\right|\right)$$

where X is the output (either n_{total} or PP), θ is the baseline set of inputs, $\Delta\theta_j$ represents a perturbation to the jth input while holding all other inputs at their baseline values (where Δ is a sensitivity factor, here equal to 10%). The metric $S_{X,j}$ represents the sensitivity of output X to jth input, averaging over positive and negative changes in the input. For cases where the inputs were discrete (i.e., t_{span} and t_m) we used a one year change. A value of one for $S_{X,j}$ indicates that the perturbed parameter changes proportionally with the perturbation, and values greater than one serve to identify sensitive parameters.

UNCERTAINTY QUANTIFICATION

Uncertainty estimates around the model predictions of the different production metrics were determined. We considered the uncertainty associated with inputs, i.e. the observed fish density $n_{obs,i}$, as well as model parameters m_{ref}, t_{span}, t_m, L_∞, k, a, and b. We assigned probability distributions to these inputs, and then determined the output distributions using Monte-Carlo simulation (Rubinstein and Kroese 2011). That is, we draw samples from the specified input distributions and apply the model to determine output samples from which we can derive distributional properties.

All model inputs were included in the uncertainty analyses, with the exception of t_0 (from the von Bertalanffy growth function, because it is simply an offset for the initial condition for length, and has a low sensitivity). Marginal probability distributions were assigned to each input and included log normal ($n_{obs,i}$, m_{ref}, k), truncated log normal via rejection sampling (L_∞, a, b), and discrete distributions (t_{span}, t_m). Log normal distributions were used to restrict the distribution to positive values, with truncations based on knowledge of parameter ranges from the literature (Froese and Binohlan 2000, Froese 2006). Discrete distributions were appropriate for parameters with discrete time steps. For all inputs, the mean of the distribution was the baseline input value (Wong and Dowd 2016), and the standard deviation (SD) determined from error estimates in the literature (usually SD across studies). Relationships between SD and the mean across fish species were examined using linear regression to allow estimation of error when none were available. For the rejection sampling, sampled values of L_∞ >60% of mean L_∞ were rejected, and values of $a > 0.04$ and values of b outside 2.7 and 3.4 were rejected (Froese and Binohlan 2000, Froese 2006). For the observations $n_{obs,i}$, the variance across pooled sites and replicate transects was determined, and then adjusted with calibration factors for sampling gear and day-night differences (see further details below and Wong et al. 2016).

We also addressed the issue of known dependencies in the input quantities and their influence on the uncertainty quantification. It is well known that there exists dependence (or correlations) in fish population parameters, especially between a and b, m_{ref} and L_∞, m_{ref} and K, and L_∞ and K (correlations and their literature sources given in Wong and Dowd 2016). To take this into account we draw input samples from a joint multivariate distribution using a statistical copula, a technique that allows for using specified marginal distributions, while having the required correlation structure (Nelson 2006). We assume that parameter dependence calculated across fish species (Pauly 1980, Froese 2006) holds within species. We did not include a joint distribution for the discrete parameters t_{span} and t_m due to their highly restricted range, even though these parameters are known to be correlated (Froese and Binohlan 2000). As well, the parameter dependence of decapods is likely relevant, although we could not include this due to lack of information.

Uncertainty quantification via Monte Carlo simulations was conducted by drawing 1000 multivariate samples from the joint distributions of the inputs. The corresponding sample of model outputs was used to estimate distributional properties of the various metrics calculated. We report the median as a measure of central tendency, and the 20th and 80th percentiles as a measure for the output range (i.e. approximate 60% credible range).

MODEL APPLICATION

We applied the quantitative approaches outlined above to determine the production potential, equivalent adults, and area per recruit of fish (i.e., fish and large decapods, such as shrimp and crabs) from *Zostera marina* (Eelgrass), *Ascophyllum nodosum* (Rockweed), and associated bare habitats on the Atlantic coast of Nova Scotia (NS), Canada. The goal of the field sampling was to determine species-specific fish density and size in order to obtain the observed density of fish in at least one age class ($n_{obs,i}$), which is the model input required from field sampling. Full details of the field sites and sampling procedures are provided in Wong et al. (2016) and Vercaemer et al. (in prep, available on request). Here we provide a brief overview of the field sampling methods separately for each biogenic habitat type sampled.

Eelgrass Beds and Adjacent Bare Habitat: Field Site Description

We sampled eight Eelgrass beds and adjacent bare habitats on the south shore and eastern shore of NS. The bare habitats were defined as soft-sediments lacking biogenic structure, and were expansive mud or sand flats located adjacent to the Eelgrass beds. The Eelgrass beds sampled spanned a gradient of habitat conditions, and included a bed within a lagoon, beds in shallow water (approximately 1.5 m deep at mean high tide) with reduced water exchange, high sediment deposition, and muddy-silty sediments, as well as beds in deeper water (approximately 4-6 m deep at mean high tide) with high water exchange, low sediment deposition, and sandy sediments. All Eelgrass beds were mono-typic and continuous with little fragmentation. Sampling was conducted in July to August 2013, when Eelgrass and fish density were expected to be at a maximum (Schein et al. 2012, Wong et al. 2013). During the sampling period, shoot density ranged from 500 – 1200 shoots m^{-2}, aboveground biomass from 200 – 500 dry g m^{-2}, belowground biomass from 400 – 1200 dry g m^{-2}, and canopy height from 22.9 – 63.0 cm across the sites. Mean water temperature during the sampling period ranged from 13.5 – 22.2 °C across the sites.

Eelgrass Beds and Adjacent Bare Habitat: Fish Sampling

Fish assemblages in Eelgrass and adjacent bare habitats were sampled during the day at mid to high tide by beam trawl or visual snorkel survey. The sampling method depended on site characteristics: shallow sites were sampled using snorkel transects, while deeper sites were sampled using the beam trawl. The beam trawl (1 m wide x 0.5 m high, 5 mm mesh size) was towed by a boat for 50 m at an approximate speed of approximately 2 km h^{-1}. Two to three trawls were conducted at each site and habitat combination. At the end of each tow, fish were emptied from the trawl into tanks onboard the boat. Fish were identified to species, counted, and measured prior to release. Snorkel transects were conducted by individuals snorkeling 30-90 m long x 1 m wide transects. The transects were run using GPS and compass bearings, with transect width delineated by a 1 m long plastic bar held perpendicular to the transect while swimming. Observers swam slowly on the surface at 0.03-0.08 m s^{-1}, adjusting swimming speed according to seagrass density and manipulating the canopy to observe hidden fish when necessary. Fish observed along the transect were identified to species, counted, and size was estimated. Data were recorded on a dive slate. Six to 16 snorkel transects were conducted at each habitat and site combination. Examination of the data indicated that species density and species richness did not change with increased replication or area sampled.

In an attempt to identify fish not captured by the trawl or visual transects, we also deployed unbaited fyke nets (5.5 m long leader with 3.2 m long chamber consisting of 5 hoops 0.6 m diameter, 4 mm x 4 mm mesh) at some site and habitat combinations. Fyke nets were set for 24 h, after which the captured fish were removed from the net, identified to species, counted, and measured prior to release. These data were used for data calibration (see below).

Rockweed Beds and Interspersed Bare Habitat: Field Site Description

We sampled four Rockweed beds and the bare habitats within the bed at two sites on the eastern shore of NS and two sites on the south shore. The bare habitats within the Rockweed beds were defined as bare bottom patches that lacked biogenic structure. These areas were comprised of boulders, cobble, and gravel interspersed with mud and sand sediment. Sampling was conducted in July-August 2015 and May-September 2016. The dominant macrophyte at all sites was Rockweed, although *Fucus* sp., green filamentous algae, green and brown turf algae, and corraline and encrusting algae were also often present. The beds were mostly continuous, and were not subjected to Rockweed harvesting. The beds were all 1 – 1.5 m deep at mean high tide with *A. nodosum* fronds exposed at low tide. Water temperature ranged from 10.3 to 21.5 °C and salinity from 27.4 to 30.0 ppt across the sampling period and all sites. Canopy height was 50 to 80 cm.

Rockweed Beds and Interspersed Bare Habitat: Fish Sampling

Fish assemblages in Rockweed beds and interspersed bare habitats were sampled biweekly during the day at mid to high tide using visual snorkel transects. Transects were approximately 100 m long x 1 m wide and conducted as for Eelgrass beds. Fish were identified to species, counted, and size was estimated, all *in situ*. Each fish observation was identified as either within the Rockweed canopy or on the bare habitat where Rockweed was absent.

Our previous work in Eelgrass suggested that visual detection of fish in the Rockweed beds was likely restricted by the thick macrophyte canopy. We thus used a fyke net to obtain estimates of fish density that were not reliant on visual detection; these estimates were used in the data calibration process (see below). Although trawling (such as that done in the Eelgrass bed) would have provided a better estimate of fish density, large cobbles and boulders at the Rockweed sites precluded this. The fyke net (4.5 m long chamber with 1 x 1 m opening and 4 frames 0.8 x 0.8 m, with 20 m long x 1.5 m high leaders from both sides of the chamber) was deployed bi-weekly from July-August 2016 at one field site. The leaders were set 10 m apart in the mid-intertidal and extended perpendicular to the shoreline 20 m seawards. The last seaward 5 m of the leaders were angled inward to a width of 1 m (the width of the chambers) and the chambers were attached at high tide. This effectively fenced off a known area of the Rockweed bed during high tide, and as the tide dropped, fish in the fenced area were forced to swim into the chambers and were captured. The chambers were collected at low tide, and the captured fish were identified to species, counted, and measured prior to release. These data were used to calibrate visual estimates of fish density obtained from the transects at all sites (see below).

Fish Age, Density, Data Calibrations, and Final Data for Model Input

Captured fish were classified into different age classes based on size estimates from the regional literature (Wong et al. 2016). The majority of fish were within the first year of their life, although there were a few instances where fish in multiple age classes were present. In these cases, year one equivalents were determined using the age distribution from the Leslie-matrix.

Species-specific fish density captured was determined for each replicate by dividing the total number of fish observed in each snorkel transect, trawl, or fyke net by the area sampled by the gear.

For Eelgrass beds and adjacent bare habitats, the field data collected were calibrated for differences in fish density estimated from the two sampling methods (i.e., visual surveys and trawls) and to account for day and night differences. The gear calibration was determined from a separate experiment where visual transects and trawl transects were conducted at two sites

within the same time period to estimate fish density. Calibration ratios were determined by dividing species-specific mean density from snorkel transects by mean density from the trawl transects. Calibration ratios indicated that visual transects underestimated the catch density of most benthic fish and that the trawl did not adequately capture pelagic species (e.g., Pollock) or fish smaller than the trawl mesh (e.g., Elvers). Data were adjusted using the species-specific calibration ratios to account for these differences. When the fyke net data indicated a species was present but was not captured by the trawl or snorkel transect, the mean density of that species across all other sites was added to the dataset.

A calibration exercise to account for day-night differences in Eelgrass beds was also conducted. At one site, trawl transects were conducted in both the day and night. Calibration ratios (species-specific fish density in the day divided by density in the night) indicated that some species were most prevalent during the night in Eelgrass (e.g., Eel, Green Crab, sculpin, pipefish). A night dataset was generated by applying these calibration ratios to the day data. Final data were determined by averaging across the day-night datasets.

For Rockweed beds, the field data were calibrated using estimates of catch density obtained from the fyke net. Calibration ratios (i.e., density of fish estimated from the fyke net divided by density from visual surveys) indicated that the visual surveys underestimated density of most benthic fish, that snorkel transects missed certain species entirely, and only snorkel surveys detected pelagic species. Data were adjusted to account for these differences using the calibration ratios. Data were not calibrated for day-night differences in Rockweed beds.

For all habitat types, final input data for the model were the mean calibrated, age-0 equivalents, species-specific density across all field sites (Wong et al. 2016, Vercaemer et al. in prep). Data from Rockweed habitats were also averaged across the two sampling years.

Fish Density Estimates, Gear Capture Efficiency, and Visual Detection Probability

Despite the data calibration, the estimates of fish density are likely biased in that they underestimate true values. There are a number of reasons for this bias. Firstly, estimates from trawl transects do not account for trawl capture efficiency, which depends in part on fish response to sound, visual detection, and body size (Wardle 1993). Also, visual detection during snorkel transects is influenced by site conditions, and although we attempted to account for this by adjusting swimming speed and manipulating the plants, detection remained limited. Lastly, our data sets are limited to one or a few years, and do not account for inter-annual variability in recruitment. The estimates of fish density in this study could be improved by future work that determines gear capture efficiencies, estimates distance sampling and visual detection probabilities, and builds extensive multi-year data sets.

COMPARISONS OF HABITAT SPECIFIC ESTIMATES OF PRODUCTION

Estimates of production (i.e., PP, EA, APR) were compared between Eelgrass and bare habitat adjacent to the Eelgrass bed, and between Rockweed and bare habitat patches within the Rockweed bed. The percentage production potential of a species increased by Eelgrass or Rockweed relative to bare habitat was calculated as $(100 \times (PP_{EG,RW} - PP_{bare}) / PP_{bare}$, where $PP_{EG,RW}$ and PP_{bare} are total production across the lifespan of the fish in Eelgrass or Rockweed and bare habitat, respectively. Negative values indicate that production was estimated to be greater on bare habitat relative to Eelgrass or Rockweed.

Production to biomass ratios predicted from the model ($P:B_{model}$) were compared to those from the regional literature similar in water temperature and other conditions ($P:B_{literature}$). The $P:B_{model}$ were determined using mean production and mean biomass across certain age classes (i.e., full population, mature or immature age classes), depending on the species. This allowed

comparison to $P:B_{literature}$ that were specific to these portions of the population. For crabs and shrimps, $P:B_{literature}$ (Heck et al. 1995) were calculated using the empirical relationship between P:B and lifespan (Robertson 1979). $P:B_{literature}$ for commercial fishes and lobster (Zhang and Chen 2007, Araújo and Bundy 2011) were calculated assuming P:B equals total mortality (fishing + natural mortality) under the assumption of steady state (Allen 1971). Here, fishing mortality was known and natural mortality was estimated from standard stock assessment analyses or empirical relationships (Pauly 1980, Hoenig 1983). For some non-commercial species, $P:B_{literature}$ (Randall and Minns 2000) were determined using allometric relationships between P:B and lifespan or weight at maturity.

PRELIMINARY REVIEW OF REGIONAL FISH DATA FOR MARITIMES CANADA

We obtained all the available datasets (to our knowledge) of fish assemblages in Eelgrass beds in Maritimes Canada. These include datasets from Atlantic NS, Southern Gulf of St. Lawrence, and PEI (Appendix A - Table A1). We summarize the main components of these datasets at the end of the results section, and illustrate their potential and difficulties in developing regional benchmarks of fish productivity.

RESULTS

FIELD DATA USED FOR MODEL APPLICATION

A total of 22 species of fish (5 crustacean species, 17 fishes) were captured in Eelgrass beds and on bare habitat (Figure 1). Nine species (Sand Lance, Eel, Silverside, Tomcod, Pollock, Winter Flounder, White Hake, Rock Crab, and Lobster) hold commercial status in Maritimes Canada (NB, NS, PEI). Almost all species were found in both habitat types, except for Rock Crab, Snailfish, Scad, and Threespine Stickleback (in Eelgrass only) and Sand Lance and sea raven (on bare only). The fish captured use the habitat in a variety of ways, with some predominantly using inshore habitats their entire lifecycle, some migrating offshore in the winter or between fresh and salt water, and others only using the inshore as juveniles (see Wong et al. 2016). Mean density of fish ranged from 5.4×10^{-4} to 12.6 m^{-2} across both Eelgrass and bare habitat. Densities were typically highest in Eelgrass compared to bare habitats, although there were a few exceptions (Green Crab, Sand Shrimp, Lobster, Silverside).

A total of 23 species of fish (5 crustacean species, 18 fishes) were captured in Rockweed beds and on bare habitat (Figure 1). Thirteen species (Rock Crab, Lobster, Sand Lance, Eel, Tomcod, Silverside, Pollock, Winter Flounder, White Hake, Smelt, Mackerel, Herring, Cod) are commercial species in the Maritimes. Several of these species were not observed in Eelgrass ecosystems (Jonah Crab, Mummichog, Cod, Herring, Mackerel, Smelt). The variety of habitat use described for Eelgrass beds was also observed for the fishes captured in Rockweed beds. Mean density of fish ranged from 3.0×10^{-5} to 0.713 m^{-2} across both Rockweed and bare habitats. Several species were only observed in Rockweed and not on bare (Lobster, Eel, Mummichog, Rock Gunnel, Cunner, White Hake, Three and Fourspine Stickleback, Cod). When species were observed in both habitats, density was consistently higher in Rockweed than in the bare.

For species captured in both Eelgrass and Rockweed, densities were usually highest in Eelgrass. The exceptions were White Hake, Silverside, and Eel, which had higher density in Rockweed than in Eelgrass. Differences in density between habitat types could indicate preferential habitat selection, but may have also resulted from the differing detection probabilities in each habitat and/or differing interannual variability across the years sampled.

MODEL ESTIMATES OF PRODUCTION POTENTIAL, EQUIVALENT ADULTS, AND AREA PER RECRUIT

We present three potential metrics of production estimated for each fish species in the different habitat types (Figures 2 and 3). These include production potential (PP), equivalent adults (EA), and area per recruit (APR).

In Eelgrass and adjacent bare habitat, the median production potential of fish species estimated by the model ranged from 8.3×10^{-3} to 46.8 g wet weight (WW) m^{-2} y^{-1} in Eelgrass and 5.9×10^{-4} to 135.2 g WW m^{-2} y^{-1} in bare habitat (Figure 2). Total production potential (i.e., sum of species-specific median production) of the entire fish community found in Eelgrass and bare habitat was 155.2 and 154.1 g WW m^{-2} y^{-1}, respectively (Table 2). Ninety percent of the PP on bare habitat was from one species (Green Crab). The total production potential of all CRA species found in Eelgrass and bare habitat was 82.6 and 16.7 g WW m^{-2} y^{-1}, respectively. Fishes in Eelgrass beds with PP ≥ 1 g WW m^{-2} y^{-1} include Rock Crab, Green Crab, Lobster, Tomcod, Grubby, Pollock, Winter Flounder, White Hake, and Three and Fourspine Stickleback. Species with high PP on bare habitats were restricted to Green Crab, lobster, and winter flounder. The PP of some species (Pipefish, Eel, Rock Gunnel, Silverside, Threespine Stickleback) were determined mainly by their field density (i.e., points lie close to the 1:1 line in Figure 4), although the PP of many other species was not directly related to field density. For these species, certain life history parameters are likely more important than field density in determining PP, but could not be identified here.

In Rockweed and interspersed bare habitat, median production potential per species ranged from 0.004 to 28.2 g WW m^{-2} y^{-1} in Rockweed and 0.003 to 20.0 g WW m^{-2} y^{-1} in bare habitat (Figure 3). Total production potential (i.e., sum of species-specific median production) of the entire fish community in Rockweed and bare habitat was 49.5 and 20.8 g WW m^{-2} y^{-1}, respectively (Table 2). Total production potential of all CRA species found in Eelgrass and bare habitat was 13.3 and 0.80 g WW m^{-2} y^{-1}, respectively. Fishes in Rockweed beds with PP ≥ 1 g WW m^{-2} y^{-1} include Green Crab, Sand Lance, Eel, Mummichog, Fourspine Stickleback, and Cod. In the bare patches within the Rockweed beds Green Crab had high PP. Similar to Eelgrass beds, the PP of some species in Rockweed beds (Pipefish, Threespine Stickleback, Rock Gunnel, Silverside, Sand Lance, and Eel) were mainly determined by their field density (Figure 4). Interestingly, the PP of these species was also identified as being determined by field density in Eelgrass beds (with the exception of Sand Lance).

Estimates of the number of equivalent adults (EA) across all species were below 3 m^{-2} for both Eelgrass and Rockweed habitats (Figures 2 and 3). Total number of equivalent adults (i.e., sum of species-specific median EA) in Eelgrass was 9.8 and 0.429 m^{-2} for the total fish community and CRA species, respectively (Table 2). Total number of equivalent adults in Rockweed was 5.7 and 0.2 m^{-2} for the total fish community and CRA species, respectively. Species where EA were above 1 m^{-2} included Green Crab, Sand Shrimp, Grubby, and Fourspine Stickleback in Eelgrass, and Green Crab, Mummichog, and Fourspine Stickleback in Rockweed. Habitat comparisons observed for PP within each species are generally the same as those for EA in both Eelgrass and Rockweed systems. For example, Pollock PP and EA are both higher in Eelgrass than in bare. However, relative differences between species are sometimes apparent when the two indices are compared. For example, the PP of Lobster in Eelgrass is much higher than Grass Shrimp, however, the opposite is observed for EA. This highlights the fundamental difference between the two indices, where PP is based on production (g WW m^{-2} y^{-1}) while EA is based on number of mature adults (num. m^{-2}).

Median area per recruit (APR) estimates ranged from 0.38 to 5.5×10^4 m^2 in Eelgrass and 0.44 to 1.4×10^5 m^2 in Rockweed, across all species (Figures 2 and 3). Larger values are apparent

for species at low density. These species often use the habitats studied but prefer other habitat types not included in this study. For example, APR is large for Lobster in the habitats we sampled because they are present at low density, preferring more rocky-cobble substrates. Smaller APR values are associated with small species that occur at high density (Mummichog, Stickleback, Sand Shrimp, Green Crab). The range of APR observed in our study ($1 - 10^4$ m^2 in Eelgrass and $1 - 10^5$ in Rockweed) is larger than that observed for freshwater ecosystems (100-1000 m^2) when all species are included. However, if species with known preferences for habitats outside of those sampled, or species at very low density are removed, the range of APR narrows considerably ($1 - 10^3$ m^2 in both Eelgrass and Rockweed).

There was overall good agreement between $P:B_{model}$ and $P:B_{literature}$ in both Eelgrass and Rockweed, although the scatter around the 1:1 line was smaller for Eelgrass (Figure 5). This agreement was evident even though $P:B_{model}$ does not include fishing mortality whereas $P:B_{literature}$ does. In Eelgrass, the only bias was observed for mature White Hake and Lobster in Eelgrass, where $P:B_{model}$ underestimated literature values. However, in Rockweed, $P:B_{model}$ underestimated literature values for mature Cod, the whole population of Cod, Lobster, mature Herring, and mature White Hake, while it overestimated literature values for immature Cod and immature Herring. This suggests that the population and growth parameters used could be improved.

INCREASED PRODUCTION POTENTIAL IN EELGRASS OR ROCKWEED RELATIVE TO BARE HABITAT

Production potential was much higher in Eelgrass and Rockweed compared to associated bare habitats (Figure 6). This was particularly pronounced for Eel, Tomcod, Pollock, Pipefish, White Hake, and Fourspine Sticklebacks in Eelgrass, and Sand Lance, Eel, Rock Gunnel, Cunner, Smelt, Mackerel and Cod in Rockweed. The percentage of increased production was similar for both Eelgrass and Rockweed, although more species were observed only using Rockweed (8 species) than those only using Eelgrass (4 species). Increased PP by bare habitat relative to Rockweed or Eelgrass was observed for some species (i.e., Green Crab, Sand Shrimp, Lobster, Silverside, Rock Gunnel, Cunner, and Rock Crab). However, these percent increases were much lower than for other species in Rockweed or Eelgrass.

MODEL SENSITIVITY AND UNCERTAINTY QUANTIFICATION

The sensitivity analysis indicated that estimates of *PP* for all species were highly sensitive to changes in model parameter *b* (associated with the nonlinear allometric length to weight relationship), with sensitivities ranging from 3 to 21 (Table 3). *PP* was also moderately influenced by changes in L_∞ (sensitivity around 3) and to a lesser extent *k* (sensitivity around 1). Production potential and n_{total} were not sensitive to any other model parameters (sensitivity < 1). Perturbations to the observations $n_{obs,i}$ resulted in proportional changes in n_{total} since the observed density simply scales the proportional age distribution. This is also the case for the model parameter *a* which results in proportional changes in *PP*.

Monte Carlo simulations provided estimates of uncertainty associated with the model inputs (Figures 2 and 3). Error estimates are highly skewed but appear nearly symmetrical on the log scale used in the figures. The right skewed distributions of estimated PP, APR, and EA likely arose from use of the lognormal distributions for several model parameters. Estimated errors were either the same order of magnitude or slightly greater than median values. Inclusion of parameter dependence (using statistical copulas) reduced the range of plausible values by 5 to 55% compared to when parameters were considered to be independent (Wong and Dowd 2016).

REVIEW OF REGIONAL NEARSHORE FISH DATA

In addition to the data of fish capture density in Eelgrass and bare habitat from the Atlantic coast of NS (as discussed above), three other datasets of fish assemblages in Eelgrass from the Maritimes Region are available across NB and PEI (Figure 7, Table 4). These data may be useful for developing regional benchmarks, yet differ widely in the methods used and information available. Below we present a summary of these data, highlighting aspects that may be useful or problematic for benchmark construction, and provide preliminary comments on their potential use in developing regional benchmarks. In all cases, the capture efficiency of the gear was assumed to be 1; densities were computed by the catch divided by the area swept by the sampling gear.

Dataset 1: Skinner and Courtenay (Skinner 2013)

Skinner and Courtenay sampled fish density in Eelgrass beds at 5 sites (Baie St. Simon Nord, Baie St. Simon Sud, Tabusintac, Neguac, Richibouctо) located along 125 km of the NB coastline (Figure 7, Table 4). These sites all have similar water depth and temperature, bottom type, salinity and level of anthropogenic influence. Different distances from an oyster aquaculture lease at each site were sampled although we only include 300-500 m distances here. A beam trawl was used to sample the fish assemblages; the trawl measured 1 m width x 0.5 m height with 5 mm mesh size and was towed for 50 m at a speed of 3-4 km h^{-1}. Sampling was conducted in June, August and September in 2006 (Baie St. Simon Sud, Tabusintac, Richibouctou) and in August 2007 (all 5 sites). Data available include species-specific density for fish and large crustaceans for all sampling dates, species-specific ash free dry weight (AFDW) in each sample for September 2006 and August 2007, and Eelgrass density and biomass.

A total of 18 species were captured, including 14 fishes and 4 crustaceans (Table 5). The species comprising ≥ 20% of the total catch were Fourspine Stickleback (23.6%) and Sand Shrimp (*Crangon septemspinosa*) (45%). Other common species included Threespine Stickleback (8.3%), *Gasterosteus* sp. (4.9%), Ninespine Dticklebacks (1.47%), and Grass Shrimp (11.13%). Commercial species captured included Eel, Silverside, Smelt, founder, and Rock Crab. Typically, fish catch was highest in August and September, although this was species dependent (Skinner 2013). Fish assemblages examined using unconstrained ordination (nMDS) showed that assemblages in Baie St. Simon and Tabusintac were similar but differed from the assemblage at Richibouctou, mainly due to the high density of sand shrimp captured (Skinner 2013) (Figure 8).

Dataset 2: Locke and Bernier

This study sampled fish communities in Eelgrass beds in several estuaries and bays of the southern Gulf of St. Lawrence in 2001-2003, 2010, and 2012 in PEI, NB, and NS (Figure 7, Table 4). Not every site was sampled each year. Most sampling took place in July and August. Sampling was conducted using a beach seine measuring 30 m long x 2 m wide with 6 mm mesh and a central bag. One end was fixed on shore and the other was walked out perpendicular to shore, walked parallel to shore and then returned to shore. The seine covered an area of 225 m^2. Data available include species-specific density for fish and large crustaceans, percent cover of Eelgrass or other submerged aquatic vegetation, aboveground biomass, and temperature and salinity.

Twenty fishes and two crustacean species were captured in total (Table 5). Species comprising ≥ 20% of the total catch included Atlantic Silverside (24%) and Mummichog (32%). Other common species were Threespine Stickleback (16%), Blackspotted Stickleback (3.5%),

Fourspine Stickleback (13.6%), and Ninespine Stickleback (2.4%). Commercial species captured included Alewife, flounder, Striped Bass, Eel, skate, and Haddock. Given the large number of sites in this dataset, we established 4 zones of the southern Gulf of St. Lawrence based on broad physical oceanographic conditions (Petrie et al. 1996, Chassé pers. comm.). These include N, W, S, and E, and are relevant for this dataset and for the Community Aquatic Monitoring Program (CAMP) dataset (discussed below). Examination of fish density captured per zone can reveal patterns in fish species density, or their absence. When the fish assemblages are compared among zones using nMDS, no differences are apparent (Figure 9). Total fish density captured was not correlated with salinity or shoot density (Figure 10).

Sampling of fish assemblages at some sites, months and years overlapped with those of Skinner and Courtenay. This allowed comparison of species-specific fish density estimated from the trawl and beach seine (Figure 11). Similar to results observed for the snorkel and trawl comparisons in NS (Wong et al. 2016), the trawl did not sample pelagic species (Silverside, Alewife, Striped Bass). Density estimates were typically higher when estimated by the trawl compared to the beach seine for many species (e.g., Fourspine Stickleback, Cunner, Pipefish, crabs), although the reverse was also sometimes observed (e.g., Blackspotted Stickleback, Mummichog).

Dataset 3: CAMP (Community Aquatic Monitoring Program), M.-H. Thériault, S. Courtenay, M. Boudreau (Weldon et al. 2005, Weldon et al. 2009, DFO 2011)

This is the most comprehensive dataset available for Eelgrass fish assemblages in the Maritimes region. The Community Aquatic Monitoring Program is led from DFO Gulf Region and utilizes local community groups to sample fish assemblages in or near Eelgrass across the Gulf of St. Lawrence (Figure 7, Table 4). Thirty six bays or estuaries were sampled at 6 stations per bay between 2004 and 2011. Most sites were sampled monthly between May and September, and were conducted in bare, very low to very high cover of Eelgrass. Sampling used the same beach seine method as employed by Locke and Bernier. Data available include species-specific capture density for fish and large crustaceans, adult and age-0 size classes, and Eelgrass percent cover (determined visually using a quadrat). The majority of sampling (87%) occurred in low Eelgrass cover (<25% cover), as sampling was often conducted nearshore and close to Eelgrass beds but not necessarily inside the Eelgrass beds (Weldon et al. 2005, 2009; DFO 2011).

Over 2004 to 2011, at least 43 fishes and 6 crustacean species were captured (Table 5). Species comprising ≥ 20% of the total catch included Mummichog (33%) and Sand Shrimp (30%). Other commonly captured species were sticklebacks (4 species, 12% total), Grass Shrimp (3%), and Silversides (17.6%). Commercial species captured were Silversides, flounders, Striped Bass, Eel, Rock Crab, Smelt, Alewife, Salmon parr, Brook Trout, Rainbow Trout, Herring, Mackerel, White Hake, and skate. The geographic extent of the CAMP data extends across the zones in the Gulf of St. Lawrence described above for Locke and Bernier, and includes one additional zone of NW (northwest). A non-metric multidimensional scaling (nMDS) ordination did not reveal distinct fish assemblages per zone when analysed by year (not shown), although these analyses were preliminary in nature.

The CAMP data can be used to provide insight into variability in fish density across Eelgrass and submerged aquatic vegetation (SAV) cover, seasons, and years. Densities of some fishes were higher in Eelgrass habitat (regardless of degree of cover) compared to bare habitat (Figure 12). Some densities also increased as percent cover Eelgrass increased (Pipefish, Eel, Grass Shrimp). Monthly sampling across multiple years at most sites also allows investigation of variability on these time scales although is not examined in depth here. Further data analyses are summarized in DFO (2011).

Comparison of Field Density of Fishes Captured Across all Studies

Median density of the total fish community (i.e., fish and large crustaceans) captured in the field was highest in the CAMP data relative to the other studies (Figure 13). The CAMP dataset was the largest, and also had the largest range in fish density observed. Gulf data from Locke and Bernier tended to have the lowest captured field densities, while Gulf data from Skinner and Courtenay and NS data from Wong and Dowd tended to be similar. These patterns hold across the total fish community and when fishes and crustaceans were observed separately.

DISCUSSION

MODEL FRAMEWORK TO DETERMINE FISH PRODUCTIVITY

In this study, we present a model framework useful to determine fish production in information- and data-poor situations, as is often the case for coastal and nearshore ecosystems. Our framework consists of a Leslie matrix that yields the steady-state stable age distribution and can be scaled using field data to compute abundance and biomass of all age classes. Production is then determined by converting length to weight (from known growth and length-weight relationships) and calculating the difference in weight between successive age classes scaled by the mean density of those age classes (Wong and Dowd 2016). Error estimates are provided via uncertainty quantification from Monte Carlo simulations that include parameter dependence.

Our model framework allows fish production to be estimated from the minimal field data typically available for nearshore ecosystems, usually consisting of fish density in one or more age classes. We estimate habitat-specific contributions rather than production on larger spatial units because it is well recognized that structured nearshore habitats are used by fishes to enhance growth and survival (Gillanders et al. 2003). In fact, we observed several commercial fishes preferentially utilizing Eelgrass and Rockweed beds instead of bare habitat, including White Hake, Eel, Pollock, flounder, Herring, Mackerel, Smelt and Cod. Fish in nearshore habitats likely make important contributions to both inshore and offshore fisheries, and estimating fish production derived from nearshore habitats is thus relevant for FPP. Furthermore, many projects (such as infilling, dredging, building of roads, or outflows) will potentially impact nearshore habitats and associated fisheries production. Our model framework allows estimation of fish production in nearshore habitats in the absence of comprehensive datasets. This provides appropriate metrics that can inform FPP decision making for authorization and offsetting.

Our model framework incorporates a high degree of generality and flexibility, allowing application not only in data-poor situations but also when more comprehensive data are available. For our study, we simplified the general framework by assuming steady state. However, the Leslie-matrix is the basis for the time dependent age structured population models (Equation 1) and is therefore suitable for the synthesis of more extensive, multi-year datasets. Similarly, we used size-dependent functions for survival and fecundity, but more complex functions can be used to incorporate density dependence, environmental forcing, and immigration/emigration. Finally, the model output of species-specific density and biomass per age class is flexible in that it can be used to formulate different indices of fish production useful for FPP decision making. The approach thus has application beyond the specific regional context provided in this study.

METRICS OF FISH PRODUCTIVITY

In this study we present three different metrics of productivity that have been previously identified as potentially useful for FPP decision making (DFO 2015). These metrics include production potential (total lifetime production of fish, similar to production foregone), equivalent adults (number of mature adults expected from a known number of fish), and area per recruit (area of habitat required to produce one mature adult). These metrics are all interrelated and represent an easy to understand "common currency" for fisheries productivity (DFO 2015). We calculated the metrics using estimated biomass (or abundance) across the lifespan of the fish, regardless if the fish utilizes the habitat for its entire lifespan or for only a portion of it. This accounts for the consequences of destroying juveniles in a habitat being broader than just the loss of juvenile biomass alone (Rago 1984, Boreman 1997). In this way, our metrics represent the maximum production that should be compensated. Our productivity metrics do not account for the effects of external pressures such as fishing or habitat degradation, although appropriate discounting could be incorporated into the survival and fecundity functions of the Leslie-matrix if desired.

The metrics presented are based on either fish production or abundance. While both production and abundance are considered useful and complementary as metrics for FPP decision making (DFO 2015), they provide fundamentally different information. Production is a more comprehensive measure than abundance because it accounts for energy flow and trophic transfer, as well as the biomass lost through death, but then made re-available through predation or scavenging. Our results show that patterns in species comparisons are dependent on whether the metric is calculated from production or abundance. For example, in seagrass, the production potential of White Hake was similar to Tomcod, yet the number of equivalent adults for White Hake was lower than for tomcod. Such differences are related to species lifespans and observed abundances. Although both fish abundance and production are considered relevant metrics of fish productivity to guide offsetting (Bradford et al. 2016), our study and others show (unsurprisingly) that production does not have a 1:1 relationship with abundance. Careful consideration should be given to which metric is most appropriate prior to use in decision making. Although equivalent adult is generally considered simpler to calculate than production (DFO 2015), our model framework allows calculation of both equivalent adult and production from the same field data (but with additional information required for growth and length-weight functions for production).

Estimates of area per recruit in our study (1 to 10^5 m^2) spanned a wider range than for freshwater fishes, which are typically 100 to1000 m^2 (DFO 2015). However, it should be noted that the freshwater data analyzed was comprised of mainly relatively common sport fish and fewer incidental or less common species. Large values in our marine data were evident for species found at low density that often prefer other habitat types than the focus habitats of this study. For example, lobster was observed in Eelgrass but prefers the rocky subtidal, and so the resultant area of Eelgrass per lobster recruit was very high. Exclusion of these somewhat anomalous cases narrows the range of area per recruit to be 1 to 10^3 m^2. Typically, area per recruit was higher for bare habitat than associated Eelgrass or Rockweed habitat.

HABITAT UNITS OF NEARSHORE FISH PRODUCTIVITY

Our study found that fish production in both Eelgrass and Rockweed was higher relative to bare habitat for the majority of species and the community as a whole. This may have resulted from habitat selection by inherently productive fish, different juvenile densities in the habitats, or from different survival and growth rates between the habitats. Our results are not surprising given that many studies have observed higher abundance, biomass and diversity of fishes in various nearshore biogenically structured habitats than in unstructured ones (e.g., Heck et al. 1989).

Species compositions in our study were similar between Eelgrass and Rockweed beds, although smelt, mackerel, Herring, and cod were only observed in Rockweed beds. Knowledge of how one habitat type increases production relative to another is useful for offsetting that involves habitat conversions (Peterson et al. 2003). Evidence from the literature and this study suggest that structured habitats have higher production of most fishes relative to unstructured habitat. However, properties of habitats and faunal communities are strongly influenced by the surrounding environmental conditions. Predictive relationships of fish production with environmental and habitat variables (i.e., water temperature, depth, salinity (Sheaves 2016, Randall et al. 2017)) would enhance our ability to understand regional differences in fish productivity beyond habitat distinctions. Decision making by FPP should recognize that habitat properties and associated faunal communities will vary according to the environmental context.

REGIONAL BENCHMARKS FROM AVAILABLE NEARSHORE FISH DATA

We reviewed all available data for fish assemblages in Eelgrass for Maritimes Canada. These data consisted of fish catch (number m^{-2}) with no information on size, age class or biomass (note the CAMP data did provide adult and age-0 classification). This makes it difficult to examine regional patterns in fish production or to estimate biomass from our model framework. Assumptions based on knowledge of juvenile inshore use and age distributions from Nova Scotia could be made to estimate biomass, but was not undertaken here. Once biomass data are obtained (either through use of our model framework or from field collections), regional patterns in fish biomass could then be examined in a similar manner to Randall et al. (2017), where parameters from models of allometry and metabolic theory of ecology are compared across regions. Use of biomass or production estimated by our model framework would be preferred over estimates of density from field surveys, because model estimates account for production of both present and absent life stages.

Using all of the datasets together to generate regional benchmarks may be problematic without accounting for differing catch efficiencies associated with the various sampling gears used. For the NS data, gear calibrations were conducted to align snorkel and beam trawl data given that trawls under sampled pelagic species while snorkel transects under sampled benthic species (Wong et al. 2016). Examination of sampling overlap in the compiled data also showed differences in capture efficiencies of the beam trawl compared to the beach seine. Prior to use in the construction of regional benchmarks, data from different sampling gears should be adjusted for different capture efficiencies.

The assembled dataset would be particularly useful to delineate fish assemblage structure among regions. It is conceivable that differing oceanographic conditions (such as those used to establish zones in the Gulf of St. Lawrence) would result in different fish communities. Our preliminary analyses using unconstrained ordination do not show strong differences in fish assemblages by these zones. However, examination of meaningful subsets of data may be beneficial. The lack of separation in fish assemblage among zones may suggest that constrained ordination, where major gradients in fish data are identified from combinations of environmental (predictor) variables, is more useful. This is not possible for datasets with no associated environmental data, although can be further examined in the CAMP data which recorded plant metrics, water temperature, and salinity at each sampling station.

The preliminary examination of the compiled data indicates that further analyses are required to evaluate its usefulness in developing relevant productivity benchmarks. The main challenge is the lack of biomass or age structure data and how to use the catch density data in a meaningful way. Regardless, the data in its current form can provide some insight into several aspects relevant to FPP decision making and offsetting. These include species composition and

assemblage structure, habitat associations, spatial and temporal variability, and estimated densities.

SUMMARY

In summary, we evaluate the potential of regional benchmarks in fish productivity for nearshore habitats by developing a model framework to estimate production, comparing production among habitat types, and reviewing available data from Eelgrass beds. Our model framework can estimate various metrics of production from minimal field data that are already available or easy to obtain. These metrics can inform development of baseline data, quantify degree of impact, determine amount of offsetting required, and be used to monitor outcomes of restoration activities. Model application using fish data from Eelgrass and Rockweed beds showed that these habitats increase fish production relative to bare habitat for almost all species, several of which are commercial species. The review of available fish data indicated that several assumptions are necessary prior to using the data in our model to estimate fish biomass or production. Nevertheless, the available fish assemblage data can provide insight into spatial patterns in fish abundance and community structure relevant for FPP decision making. Our study provides the initial steps towards developing benchmarks of fish production for nearshore habitats. Future work is necessary to identify appropriate spatial scales for benchmarks in these ecosystems and to identify predictive relationships of fish production with environmental measures.

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TABLES

Table 1. Fish population parameters used in the model to determine production potential, equivalent adults, and area per recruit of fishes from Eelgrass beds (Zostera marina), Rockweed (Ascophyllum nodosum) and associated bare habitats. The additional model input of species-specific density in at least one age class from field data is shown in Figure 1. m_{ref} = natural mortality, t_{span} = lifespan, t_m = age at maturity, L_∞ = length at infinity, K = rate at which L_∞ is approached, t_0 = time when fish has zero length, a and b = parameters in the length-weight (L-W) relationship. CW = carapace width, DW = dry weight, AFDW = ash free dry weight, WW = wet weight, CL = carapace length, TL = total length. Weight and size conversions used include: DW to WW=3.875 (Rock Crab), AFDW to WW=5.556 (Green Crab), CL to TL=4.546CL-0.816 (mm) (Sand Shrimp). Values are median ± SD. References are listed in the Appendix B.

Species	m_{ref} (y^{-1})	t_{span} (y)	t_m (y)	L_∞	K (y^{-1})	t_0 (y)	a	b	Units	References
Rock Crab (*Cancer irroratus*)	0.455 ± 0.267	8	4	180 ± 45.8	0.2 ± 0.10	-0.718	0.00006 ± 0.000022	2.938 ± 0.147	L-W (mm CW, g DW); L_∞ (mm CW)	Barbeau and Scheibling 1994, Reilly and Saila 1978, Brey 1999, DFO 2013
Green Crab (*Carcinus maenas*)	0.664 ± 0.406	6	1	91.5 ± 22.9	0.743 ± 0.385	-0.085	0.00005 ± 0.000019	2.885 ± 0.144	L-W (mm CW, g AFDW); L_∞ (mm CW)	Baeta et al. 2005, Berrill 1982, Yamanda 2005, Brey 1999
Sand Shrimp (*Crangon septemspinosa*)	1.08 ± 0.618	3.7	1	18.3 ± 4.66	0.91 ± 0.472	-0.378	0.00027 ± 0.00010	3.357 ± 0.168	L-W (mm TL, mg WW); L_∞ (mm CL)	Oh et al. 1999, Locke et al. 2005
American Lobster (*Homarus americanus*)	0.1 ± 0.062	50	4	253.5 ± 64.5	0.0674 ± 0.035	-0.434	0.000692 ± 0.00026	3.0374 ± 0.152	L-W (mm CL, g WW); L_∞ (mm CL)	Thomas 1973, Krouse 1977, Tremblay et al. 2013, French McCay et al. 2003
Grass Shrimp (*Palaemonetes vulgaris*)	3.83 ± 2.44	1.5	0.16	4.68 ± 1.19	0.48 ± 0.249	-0.8	0.012 ± 0.0045	3.174 ± 0.159	L-W (cm TL, g WW); L_∞ (cm TL)	Wong unpub., Hoffman 1980, Brey 1999, Chazro-Olvera 2009
Sand Lance (*Ammodytes americanus*)	0.59 ± 0.375	7.3	2	24.7 ± 6.29	0.39 ± 0.202	-0.37	0.0013 ± 0.00023	3.3 ± 0.166	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988, Brethes et al. 1992, Westin et al. 1979
American Eel (*Anguilla rostrata*)	0.17 ± 0.104	22.4	4.6	1241.3 ± 316.0	0.027 ± 0.014	-0.672	0.001 ± 0.00082	3.17 ± 0.176	L-W (cm TL, g WW); L_∞ (mm TL)	DFO 2014, Jessop 2004
Banded Killifish (*Fundulus diaphanus*)	1.22 ± 0.748	3.3	1	13.8 ± 3.51	0.85 ± 0.441	-0.19	0.0013 ± 0.0005	3.25 ± 0.163	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988, Smith 1939
Sea Raven (*Hemitripterus americanus*)	0.3 ± 0.176	13.1	3.1	66.3 ± 16.8	0.22 ± 0.114	-0.51	0.0183 ± 0.00689	3 ± 0.15	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988, IGFA 2001

Species	m_{ref} (y^{-1})	t_{span} (y)	t_m (y)	L_∞	K (y^{-1})	t_0 (y)	a	b	Units	References
Atlantic Silverside (*Menidia menidia*)	1.45 ± 0.882	2.7	0.8	12.8 ± 3.26	1.04 ± 0.540	-0.19	0.00602 ± 0.0022	3.023 ± 0.151	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988, Fay et al. 1983, Jessop 1983, Conover and Ross 1982
Tomcod (*Microgadus tomcod*)	0.84 ± 0.488	3.9	1	39.8 ± 10.1	0.73 ± 0.379	-0.17	0.00753 ± 0.0028	3.032 ± 0.151	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988, Stewart and Auster 1987
Grubby Sculpin (*Myoxocephalus aenaeus*)	1.1 ± 0.639	3.5	1	19 ± 4.83	0.82 ± 0.425	-0.19	0.01246 ± 0.0047	3.026 ± 0.151	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988, Roseman et al. 2005, Lazzari et al. 1989
Rock Gunnel (*Pholis gunnellus*)	0.5 ± 0.297	9.7	2.6	20.9 ± 2.7	0.29 ± 0.12	-0.63	0.0043 ± 0.00162	3.018 ± 0.151	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988, Vallis et al. 2007, Coull et al. 1989, Gunnarsson and Gunnarsson 2002
Pollock (*Pollachius virens*)	0.26 ± 0.154	14.4	3.1	101 ± 26.1	0.2 ± 0.049	-0.6	0.0095 ± 0.0015	2.99 ± 0.037	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988, DFO 2009, Bedford et al. 1986, Dorel 1986, Erzini 1991, Luccio 1967, Damas 1909, Magnussen 2007, Nikolskii 1957, Gottlieb 1957, Schmidt 1959, Jennings et al. 1998, Anonymous 1996
Winter Flounder (*Pseudopleuronectes americanus*)	0.45 ± 0.268	8.9	2.2	43.6 ± 8.07	0.32 ± 0.21	-0.47	0.0213 ± 0.008	3 ± 0.15	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988, DFO 2012, Poole 1969, Pauly 1979, McCracken 1954, Berry et al. 1965, Beverton and Holt 1959, Howe and Coates 1975, Witherell and Burnett 1993, Lux 1973
Northern Pipefish (*Syngnathus fuscus*)	0.62 ± 0.376	6.2	1.6	34.5 ± 8.78	0.46 ± 0.23	-0.29	0.0002 ± 0.000075	3.12 ± 0.16	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988
Cunner (*Tautogolabrus adspersus*)	0.37 ± 0.226	12.9	3.3	29.7 ± 5.32	0.22 ± 0.04	-0.77	0.00275 ± 0.0010	3.378 ± 0.169	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988, Serchuk and Cole 1974, Dew 1976, Johansen 1925
White Hake (*Urophysis tenuis*)	0.15 ± 0.098	26.2	5.4	136 ± 36.7	0.11 ± 0.07	-1.04	0.0042 ± 0.00022	3.16 ± 0.0141	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988, DFO 2005, Clay and Clay 1991
Dusky Snailfish (*Liparis gibbus*)	0.32 ± 0.197	13.1	3.2	54 ± 13.7	0.22 ± 0.11	-0.56	0.0104 ± 0.0039	3.06 ± 0.153	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988

Species	m_{ref} (y^{-1})	t_{span} (y)	t_m (y)	L_∞	K (y^{-1})	t_0 (y)	a	b	Units	References
Bigeye Scad (*Selar crumenophthalmus*)	1.63 ± 0.974	1.9	0.5	24.6 ± 3.6	1.51 ± 0.49	-0.11	0.0098 ± 0.006	3.18 ± 0.157	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988, Roos et al. 2007
Fourspine Stickleback (*Apeltes quadracus*)	1.42 ± 0.852	3.3	1.1	7 ± 1.78	0.83 ± 0.43	-0.29	0.01023 ± 0.003	3.09 ± 0.154	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988, Schwarz 1965
Threespine Stickleback (*Gasterosteus aculeatus*)	1.31 ± 0.764	3.5	1.1	8 ± 0.904	0.78 ± 0.99	-0.3	0.0068 ± 0.0028	3.28 ± 0.200	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988, Verreycken et al. 2011, Tarkan et al. 2006, Bertin 1923, Snyder 1991, van Mullem and van der Vlugt 1964, Worthmann 1975
Atlantic Herring (*Clupea harengus*)	0.52 ± 0.303	8.1	2.1	28.3 ± 7.20	0.35 ± 0.18	-0.48	0.0069 ± 0.002	3.04 ± 0.15	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988
Smelt (*Osmerus mordax*)	0.49 ± 0.292	8.3	2.1	32.5 ± 8.27	0.34 ± 0.17	-0.48	0.0089 ± 0.003	2.96 ± 0.15	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988
Atlantic Cod (*Gadus morhua*)	0.22 ± 0.132	16.9	3.6	106 ± 26.98	0.17 ± 0.09	-0.71	0.0079 ± 0.003	3.05 ± 0.15	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988
Mackerel (*Scomber scombrus*)	0.3 ± 0.183	14.3	3.4	47.3 ± 12.04	0.2 ± 0.10	-0.75	0.0055 ± 0.002	3.13 ± 0.16	L-W (cm TL, g WW); L_∞ (cm TL)	Fishbase 2015, Scott and Scott 1988
Jonah Crab (*Cancer borealis*)	0.455 ± 0.267	8	4	180 ± 45.83	0.2 ± 0.10	-0.718	0.00006 ± 0.00002	2.94 ± 0.15	L-W (mm CW, g DW); L_∞ (mm CW)	Barbeau and Scheibling 1994, Reilly and Saila 1978, Brey 1999, DFO 2013 (same parameters used as for Rock Crab due to lack of information)

Table 2. Total fish production potential (g WW m^{-2} y^{-1}) and total number of equivalent adults (number m^{-2}) estimated from the model framework. Equivalent adults are calculated as the sum of the number of mature adults across the entire lifespan of the fish. Estimates are provided for Eelgrass (Zostera marina), Rockweed (Ascophyllum nodosum) and associated bare habitats. Values are the sum of the species-specific median values from the Monte Carlo simulations. The 60% credible intervals are provided in the following brackets; these were determined as the sum of the species-specific lower and upper bounds from the simulations. CRA fishes include Rock Crab, Jonah Crab, Lobster, Eel, Silverside, Tomcod, Pollock, Winter Flounder, White Hake, Smelt, Mackerel, Herring, and Cod. WW = wet weight, CRA = commercial, recreational, and aboriginal fishery species.

Habitat	Species	Production Potential	Equivalent Adults
Eelgrass	Total	155.274 (58.210-420.058)	9.850 (7.260-14.154)
	CRA	82.607 (30.825-227.974)	0.429 (0.274-0.781)
Bare habitat (adjacent to Eelgrass)	Total	154.093* (46.661-522.381)	26.679 (18.714-39.538)
	CRA	16.690 (3.739-75.857)	0.413 (0.230-0.764)
Rockweed	Total	49.569 (16.250-156.627)	5.737 (1.895-24.923)
	CRA	13.318 (5.379-35.450)	0.202 (0.048-0.869)
Bare habitat (within Rockweed)	Total	20.850 (6.698-57.981)	1.269 (1.027-1.717)
	CRA	0.795 (0.311-2.213)	0.003 (0.001-0.006)

*note that 90% of this value is from one species (green crab, *Carcinus maenas*)

Table 3. Results of the sensitivity analysis for fishes in Eelgrass. Values for the sensitivity metric, S, are reported (see text), where S = 1 defines a proportional response and S > 1 denotes a sensitive input. The output quantities of interest are n_{total} and PP. Sensitivity of these is defined with respect to various inputs as designated.

	n_{total}				PP								
	m_{ref}	$n_{obs,i}$	t_{span}	t_m	$n_{obs,i}$	m_{ref}	t_{span}	t_m	L_∞	t_0	k	a	b
Rock Crab	0.78	1.00	0.05	0.03	0.50	0.83	0.18	0.13	2.95	0.38	1.84	1.00	17.93
Green Crab	0.57	1.00	0.03	0.001	0.50	0.53	0.10	0.06	2.89	0.09	1.37	1.00	15.03
Sand Shrimp	0.45	1.00	0.04	0.01	0.50	0.40	0.06	0.04	3.42	0.24	1.30	1.00	19.24
Lobster	1.25	1.00	0.01	0.001	0.50	1.59	0.45	0.23	3.05	0.12	1.75	1.00	21.20
Grass Shrimp	0.08	1.00	0.01	0.04	0.50	0.13	0.0002	0.01	3.19	0.58	1.88	1.00	3.56
Eel	1.00	1.00	0.03	0.002	0.50	1.75	0.52	0.27	3.18	0.21	2.60	1.00	13.81
Killifish	1.98	1.00	0.33	0.01	0.50	0.92	0.15	0.08	3.27	0.22	1.60	1.00	8.08
Silverside	0.29	1.00	0.03	0.003	0.50	0.30	0.04	0.03	3.03	0.17	1.35	1.00	7.43
Tomcod	0.50	1.00	0.06	0.0009	0.50	0.50	0.09	0.05	3.04	0.16	1.45	1.00	11.92
Grubby	0.39	1.00	0.04	0.002	0.50	0.41	0.07	0.04	3.04	0.19	1.48	1.00	8.68
Rock Gunnel	0.72	1.00	0.03	0.03	0.50	0.75	0.16	0.11	3.03	0.39	1.73	1.00	8.37
Pollock	1.02	1.00	0.02	0.02	0.50	0.93	0.21	0.12	3.00	0.24	1.53	1.00	15.91
Winter Flounder	0.78	1.00	0.03	0.03	0.50	0.77	0.16	0.11	3.01	0.29	1.59	1.00	11.67
Pipefish	0.61	1.00	0.03	0.01	0.50	0.68	0.14	0.08	3.13	0.26	1.66	1.00	11.18
Cunner	0.86	1.00	0.02	0.03	0.50	0.92	0.21	0.14	3.40	0.41	1.86	1.00	11.44
White Hake	1.24	1.00	0.02	0.01	0.50	1.07	0.25	0.14	3.17	0.25	1.61	1.00	19.28
Snailfish	0.91	1.00	0.02	0.02	0.50	0.94	0.21	0.13	3.07	0.29	1.67	1.00	12.78
Scad	0.27	1.00	0.10	0.001	0.50	0.22	0.02	0.01	3.19	0.11	1.22	1.00	11.07
Fourspine Stickleback	2.19	1.00	0.33	0.14	0.50	1.09	0.18	0.12	3.10	0.26	1.52	1.00	5.21
Threespine Stickleback	0.34	1.00	0.04	0.03	0.50	0.38	0.06	0.05	3.30	0.30	1.63	1.00	6.00

Table 4. Description of the different datasets of fish assemblages in Eelgrass from Maritime Canada that were examined.

Study	Location	Years	Total No. Sites	Habitats Sampled	Habitat Metrics Measured	Sampling Frequency	Sampling Gear	Fish Metrics Measured	Environmental Variables Measured
Skinner and Courtenay	NB Acadian peninsula	2006, 2007	5	Eelgrass	Shoot density, shoot biomass, canopy height, epiphyte biomass	Once/multiyear	Beam trawl	Capture density, total biomass, some sizes	See thesis
Locke and Bernier	Southern Gulf of St. Lawrence	2001-2003, 2010, 2012	30	Eelgrass	% cover Eelgrass and other macrophytes, shoot biomass, sediment type	Once/multiyear	Beach seine	Capture density	Temperature, salinity, weather, tide
CAMP	Southern Gulf of St. Lawrence	2004-2011	36	Eelgrass, bare	% cover Eelgrass and other macrophytes, sediment (% moisture, % organic	Multiyear	Beach seine	Capture density, adult and age-0	Temperature, salinity, disolved oxygen, water nutrients
Wong and Dowd	NS Atlantic coast	2013	8	Eelgrass, bare	Shoot density, shoot and root biomass, canopy height, sediment (organic content, particle size)	Once	Beam trawl, snorkel	Capture density, size	Continuous temperature, wave exposure, depth

Table 5. Percent of total capture density for each species in Eelgrass for the different datasets. A dash (-) indicates "not captured".

Common Name	Scientific Name	Skinner and Courtenay	Locke and Bernier	CAMP	Wong and Dowd
Alewife	*Alosa pseudoharengus*	-	0.35	0.12	-
Alosa sp.	*Not applicable*	-	-	0.01	-
Atlantic Salmon parr	*Salmo salar*	-	-	<0.01	-
Banded Killifish	*Fundulus diaphanus*	-	0.26	0.42	0.45
Blackspotted stickleback	*Gasterosteus wheatlandi*	0.1	3.57	2.63	-
Blueback Herring	*Alosa aestivalis*	-	-	0.01	-
Brook Trout	*Salvelinus fontinalis*	-	-	<0.01	-
Brown Bullhead	*Ameiurus nebulosus*	-	-	<0.01	-
Chub sp.	*Not applicable*	-	-	<0.01	-
Cod	*Gadus morhua*	-	-	-	-
Cunner	*Tautogolabrus adspersus*	0.68	1.51	0.11	0.04
Cyprinidae sp.	*Cyprinidae sp.*	-	-	0.01	-
Eel	*Anguilla rostrata*	0.03	0.01	<0.01	1.98
Flounder sp.	*Not applicable*	-	-	0.04	-
Fourspine Stickleback	*Apeltes quadracus*	23.62	13.65	6.44	25.9
Gasterosteus sp.	*Gasterosteus sp.*	4.92	-	-	-
Grass Shrimp	*Palaemonetes vulgaris*	11.13	0.72	3.91	0.82
Green Crab	*Carcinus maenas*	-	-	0.62	19.9
Grubby Sculpin	*Myoxocephalus aenaeus*	0.08	0.02	<0.01	6.29
Haddock	*Melanogrammus aeglefinus*	-	0	-	-
Herring	*Clupea harengus*	-	-	-	-
Jonah Crab	*Cancer borealis*	-	-	-	-
Lady Crab	*Ovalipes ocellatus*	-	-	<0.01	-
Lake Chub	*Couesius plumbeus*	-	-	<0.01	-
Lobster	*Homarus americanus*	-	-	-	0.18
Mackerel	*Scomber scombrus*	-	-	<0.01	-
Mud Crab	*Neopanopeus sayi / Xanthidae sp.*	2.31	-	0.21	-
Mummichog	*Fundulus heteroclitus*	0.61	32.27	31.05	-
Ninespine Stickleback	*Pungitius pungitius*	1.47	2.38	0.88	-

Common Name	Scientific Name	Skinner and Courtenay	Locke and Bernier	CAMP	Wong and Dowd
Pipefish	*Syngnathus fuscus*	0.16	1.09	0.1	0.45
Pollock	*Pollachius virens*	-	-	-	0.86
Rainbow Trout	*Salmo gairdneri*	-	-	<0.01	-
Rock Crab	*Cancer irroratus*	0.77	-	0.08	0.78
Rock Gunnel	*Pholis gunelus*	-	0.02	<0.01	0.10
Sand Shrimp	*Crangon septemspinosa*	45.03	0.76	30.51	11.9
Sand Lance	*Ammodytes americanus*	-	-	0.05	-
Scad (Big Eye)	*Selar crumenophthalmus*	-	-	-	<0.01
Sculpin	*Myoxocephalus sp.*	-	0.05	0.01	-
Silver Rockling	*Gaidropssarus argentatus*	-	-	<0.01	-
Silverside	*Menidia menidia*	0.25	24.08	17.64	0.95
Smelt	*Osmerus mordax*	0.03	-	0.1	-
Smooth Flounder	*Liopsetta putnami*	0.04	0.66	0.51	-
Snailfish (Dusky)	*Liparis gibbus*	-	-	-	<0.01
Striped Bass	*Morone saxitilis*	-	0.88	0.19	-
Thorny Skate	*Amblyraja radiata*	-	0	-	-
Threespine Stickleback	*Gasterosteus aculeatus*	8.34	16.62	4.09	27.0
Tomcod	*Microgadus tomcod*	0.28	0.12	0.06	1.42
Trout sp.	*Salmo sp.*	-	-	<0.01	-
Unknown	*Unknown*	-	-	0.02	-
White Barracudina	*Notolepis rissoi*	-	-	<0.01	-
White Hake	*Urophysis tenuis*	-	-	<0.01	0.05
White Perch	*Morone americanus*	-	-	<0.01	-
White Sucker	*Castotomus commersonii*	-	-	<0.01	-
Windowpane Flounder	*Scophthalmus aquosus*	-	0.06	<0.01	-
Winter Flounder	*Pseudopleuronectes americanus*	0.15	0.84	0.17	0.74
Winter Skate	*Raja ocellata*	-	-	<0.01	-
Yellowtail Flounder	*Limanda ferruginea*	-	0.07	<0.01	-

FIGURES

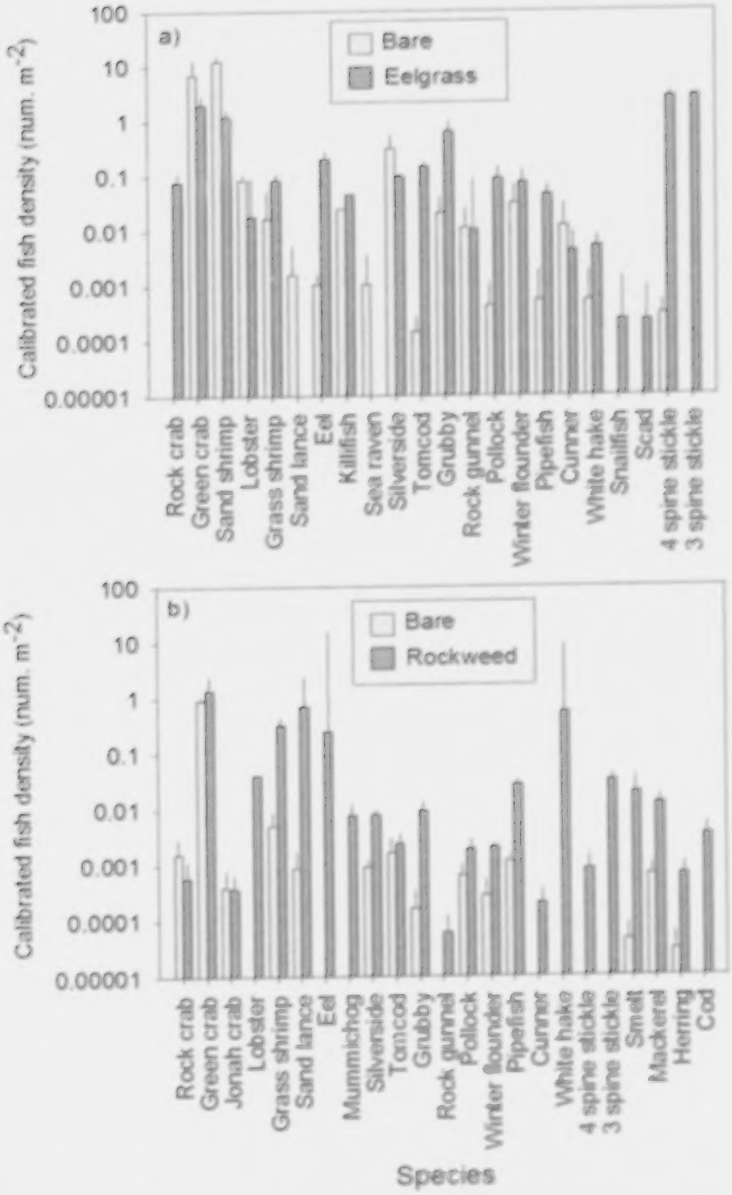

Figure 1. Fish density (mean + 1 SE) from field observations pooled across field sites in (a) Eelgrass and adjacent bare habitat (n = 8 sites) and (b) Rockweed and interspersed bare habitat (n = 4 sites). Data are calibrated to account for differences between sampling gears, day-night (Eelgrass only) and represent age-0 equivalents.

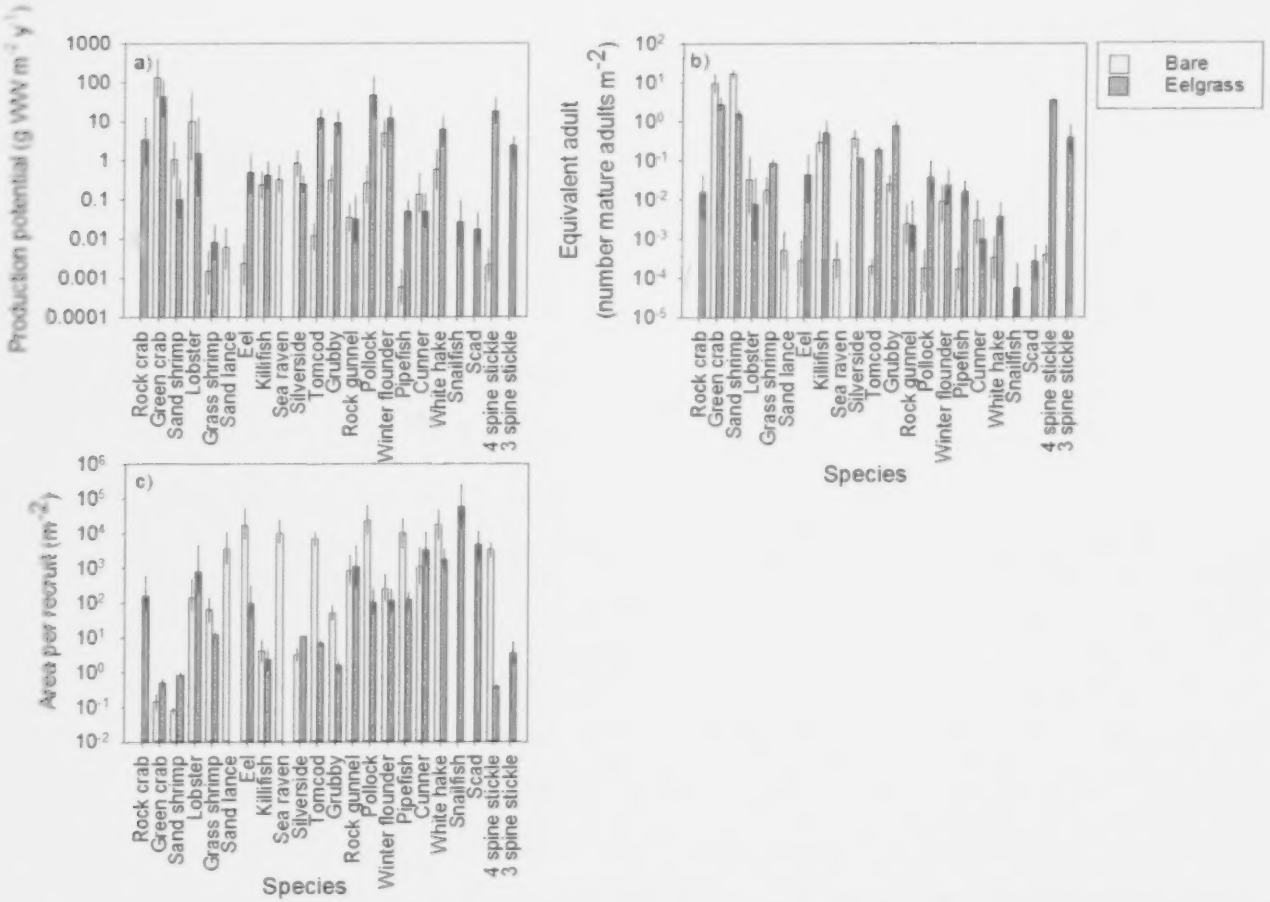

Figure 2. Median values with 60% credible intervals for (a) Production potential, (b) Equivalent number of adults, and (c) Area per recruit, in Eelgrass and adjacent bare habitat, estimated from the model framework. Credible intervals were determined from Monte Carlo simulations that included copulas for fish but not for decapods. WW = wet weight.

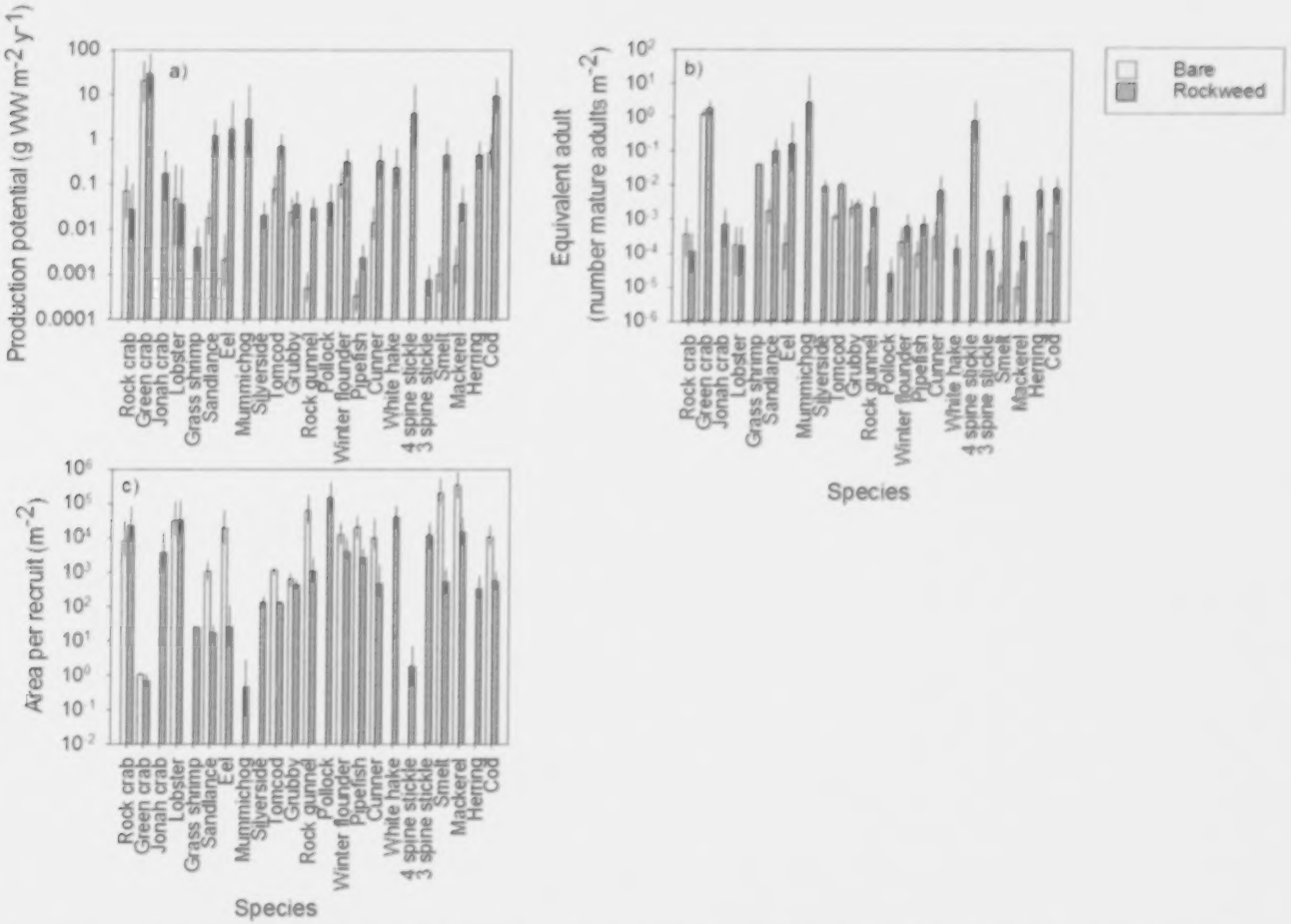

Figure 3. Median values with 60% credible intervals for (a) Production potential, (b) Equivalent number of adults, and (c) Area per recruit, in Rockweed and interspersed bare habitat, estimated from the model framework. Credible intervals were determined from Monte Carlo simulations that included copulas for fish but not for decapods. WW = wet weight.

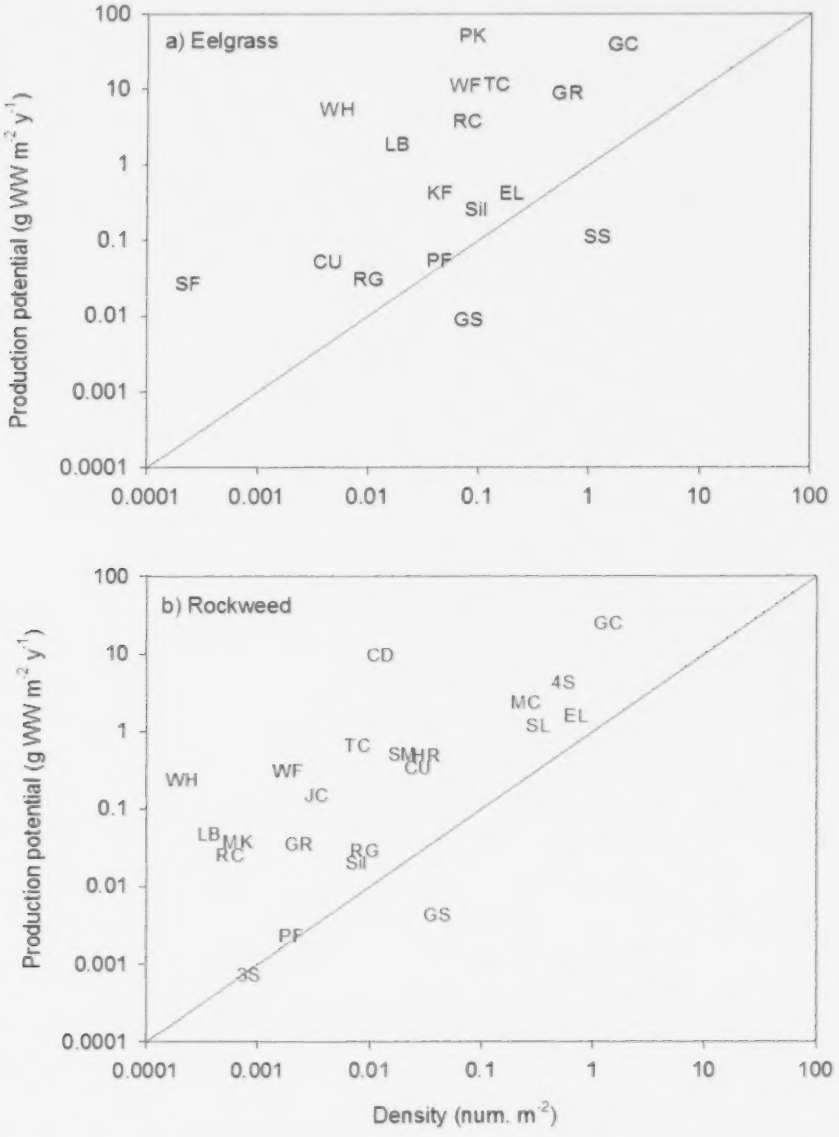

Figure 4. Field density vs. production potential in (a) Eelgrass and (b) Rockweed. The 1:1 line is shown. Labels indicate species: RC = Rock Crab, GC = Green Crab, SS = Sand Shrimp, LB = Lobster, GS = Grass Shrimp, SL = Sand Lance, EL = Eel, KF = Killifish, Sil = Silverside, TC = Tomcod, GR = Grubby, RG = Rock Gunnel, PK = Pollock, WF = Winter Flounder, PF = Pipefish, CU = Cunner, WH = White Hake, SF = Snailfish, SC = Scad, 4S = Fourspine Stickleback, 3S = Threespine Stickleback, MK = Mackerel, CD = Cod, MC + Mummichog, HR = Herring, SM = Smelt, JC = Jonah Crab.

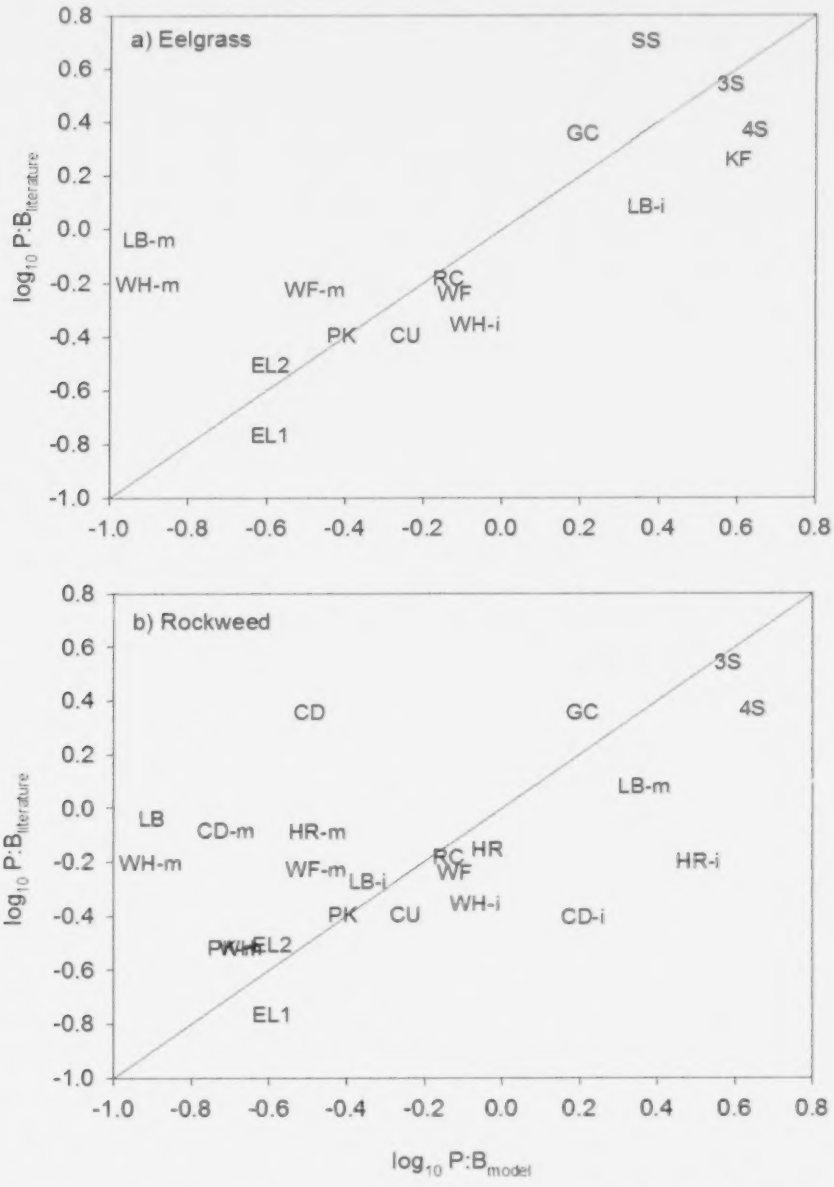

Figure 5. P:B values predicted from the model framework ($P:B_{model}$) versus those from the literature ($P:B_{literature}$). The 1:1 line is shown, and values have been log_{10} transformed. See Figure 4 for species abbreviations. q M mature, i immature; points lacking these subscripts are P:B estimates for the whole population. For Eel, numbers indicate different literature estimates.

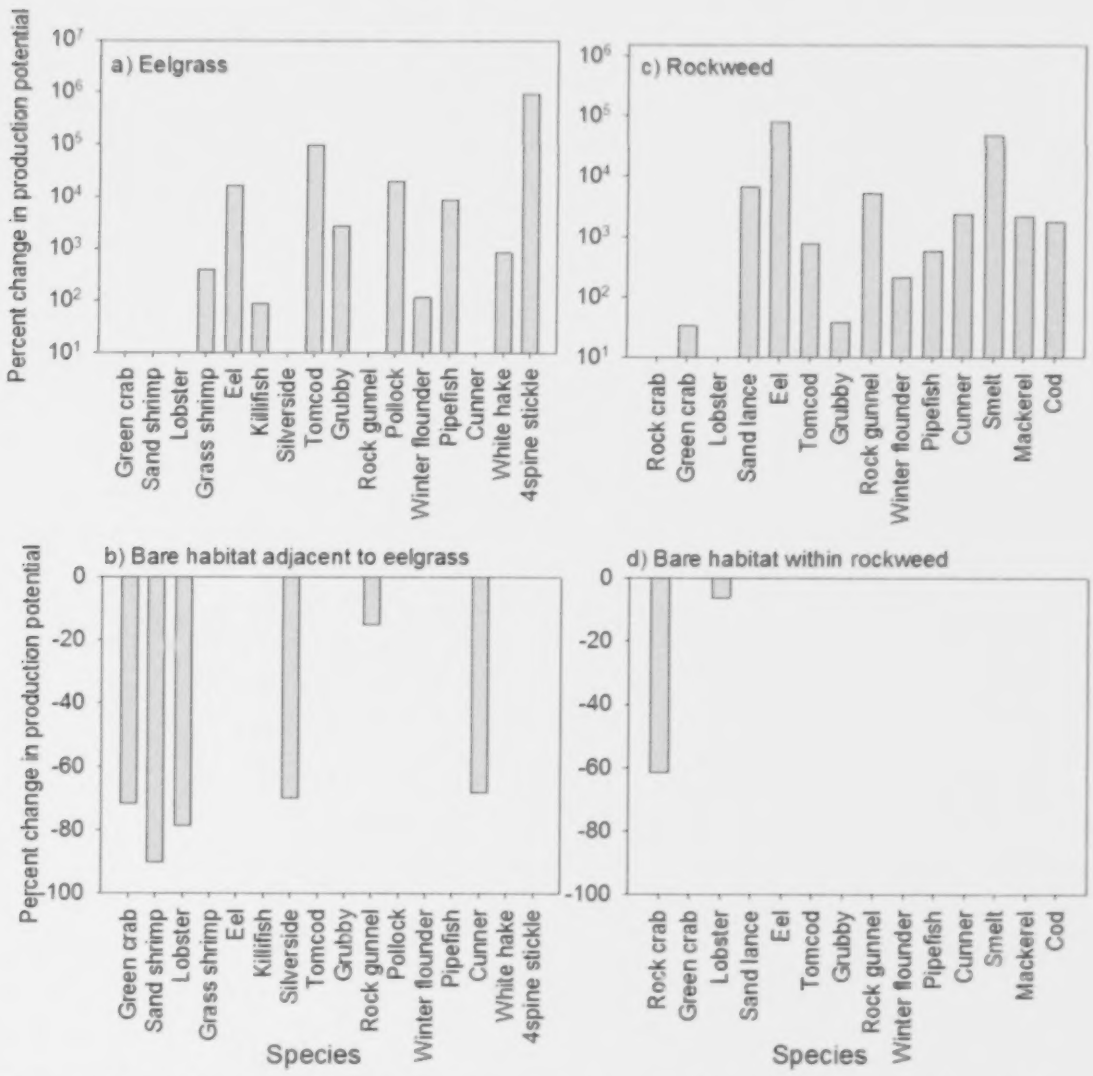

Figure 6. Percent change of median fish production potential by Eelgrass and Rockweed relative to associated bare habitats. Only species found in both habitat types are included. Values are calculated as $(100 \times (PP_{EG,RW} - PP_{bare}) / PP_{bare}$, *where* $PP_{EG,RW}$ *and* PP_{bare} *are total production across the lifespan of the fish in Eelgrass or Rockweed and bare habitat, respectively. Negative values indicate that production was greater for bare habitats relative to Eelgrass or Rockweed habitats.*

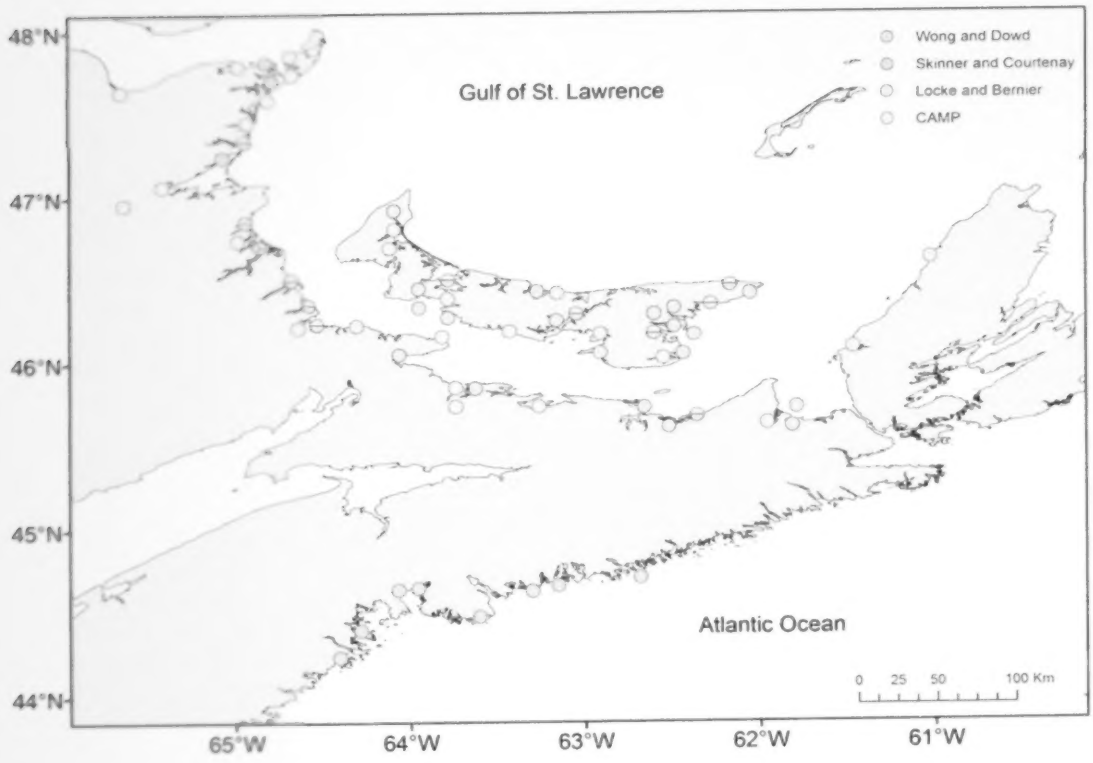

Figure 7. Sampling locations from the different datasets of fish assemblages in Eelgrass for Maritimes Canada.

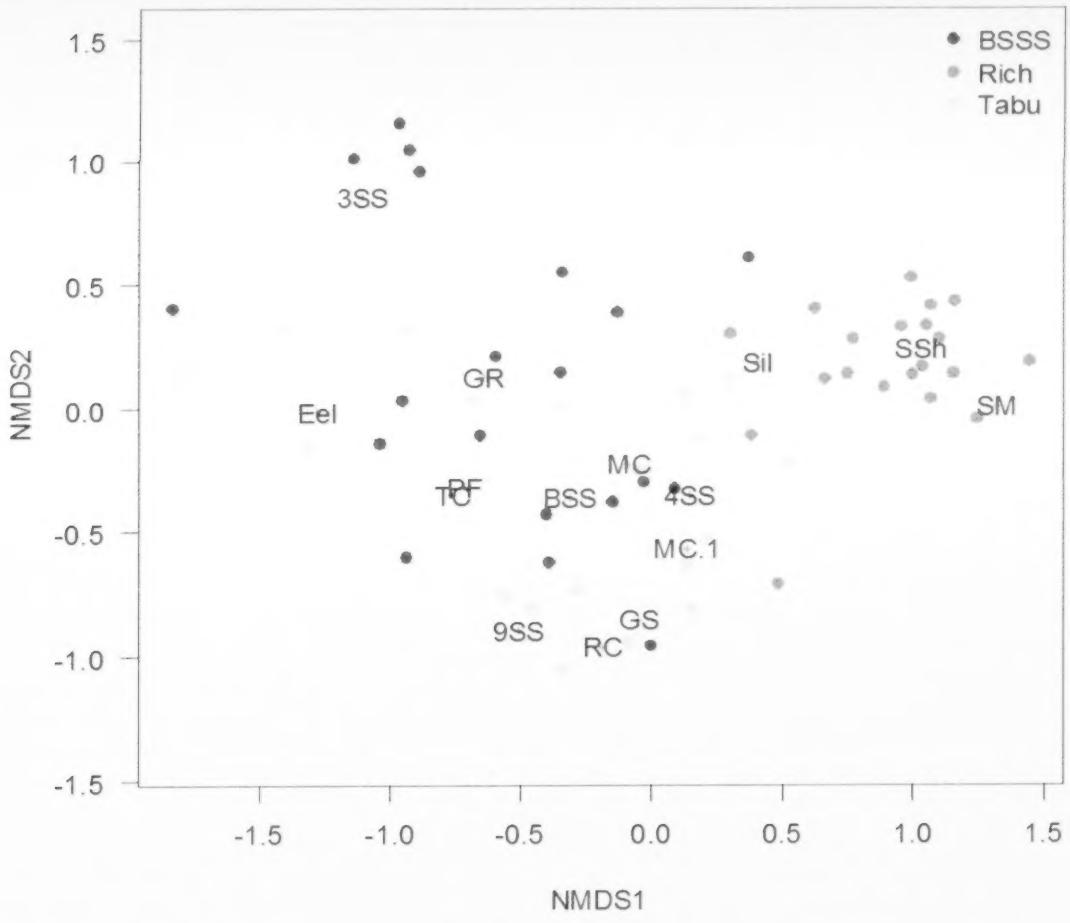

Figure 8. nMDS plot of fish community structure (based on fish capture density) from Skinner and Courtenay dataset, showing assemblage differences among Eelgrass beds at the sampling sites. Stress = 0.117. 3SS = Threespine Stickleback, 4SS = Fourspine Stickleback, 9SS = Ninespine Stickleback, BSS = Blackspotted Stickleback, TC = Tomcod, GR = Grubby, MC = Mummichog, PF = Pipefish, Sil = Silverside, SM = Smelt, SSh = Sand Shrimp, GS = Grass Shrimp, RC = Rock Crab, MC = Mud Crab.

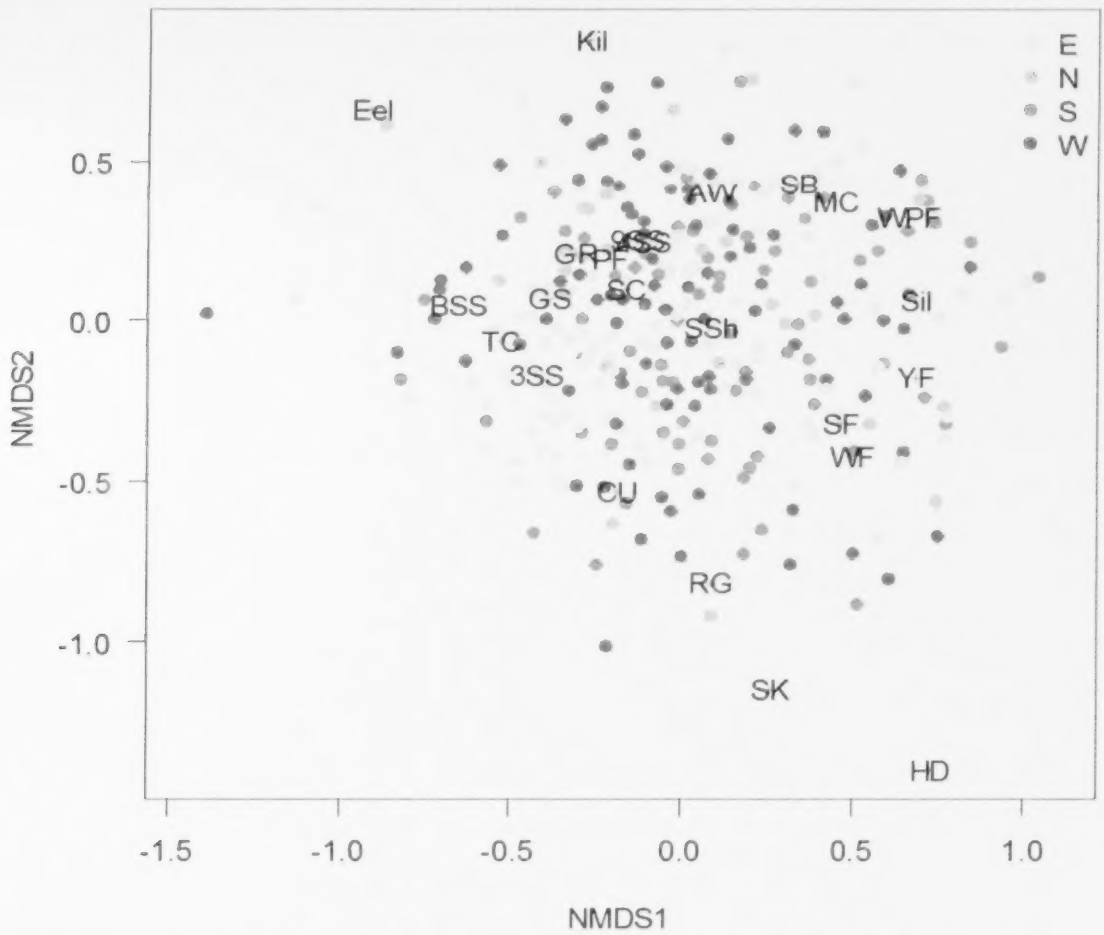

Figure 9. nMDS plot of fish community structure (based on fish capture density) from Locke and Bernier dataset, showing assemblage differences among Eelgrass beds in the different zones of the southern Gulf of St. Lawrence. Stress = 0.283. 3SS = Threespine Stickleback, BSS = Blackspotted Stickleback, 4SS = Fourspine Stickleback, 9SS = Ninespine Stickleback, Sil = Silverside, MC = Mummichog, AW = Aalewife, Kil = Banded Killifish, WF = Winter Flounder, CU = Cunner, YF = Yellowtail Flounder, SF = Smooth Flounder, SB = Striped Bass, GR = Grubby, RC = Rock Gunnel, SK = Skate, PF = Pipefish, HD = Haddock, TC = Tomcod, WPF = Windowpane Flounder, SC = Sculpin, SSh = Sand Shrimp, GS = Grass Shrimp.

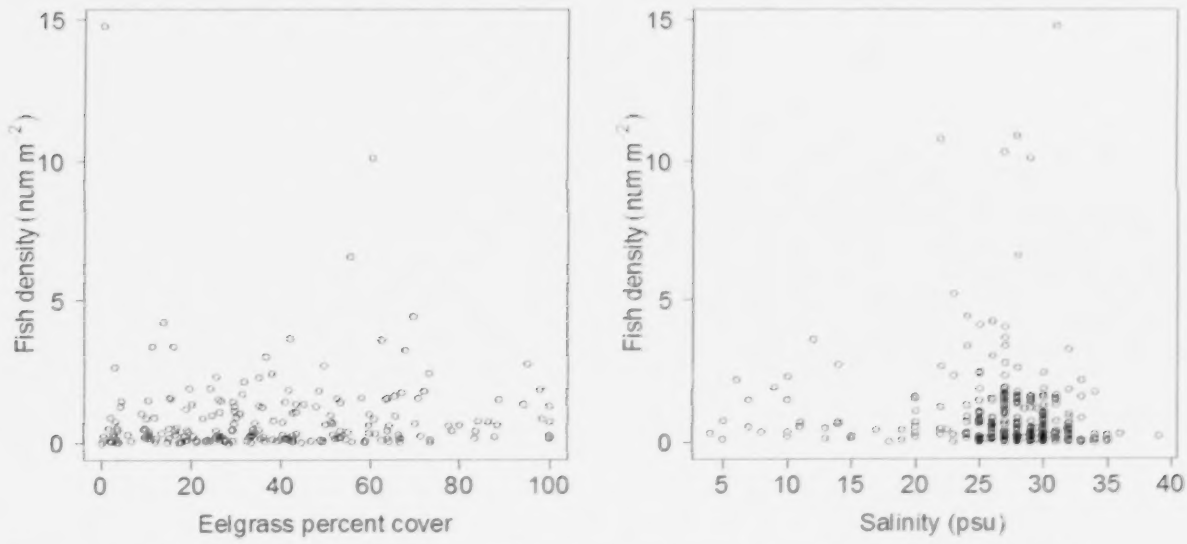

Figure 10. Total fish density captured (num. m^{-2}) vs. Eelgrass percent cover (left panel) and total fish density captured vs. salinity (right panel). Data are pooled across all sites in 2001 and 2002 from Locke and Bernier dataset.

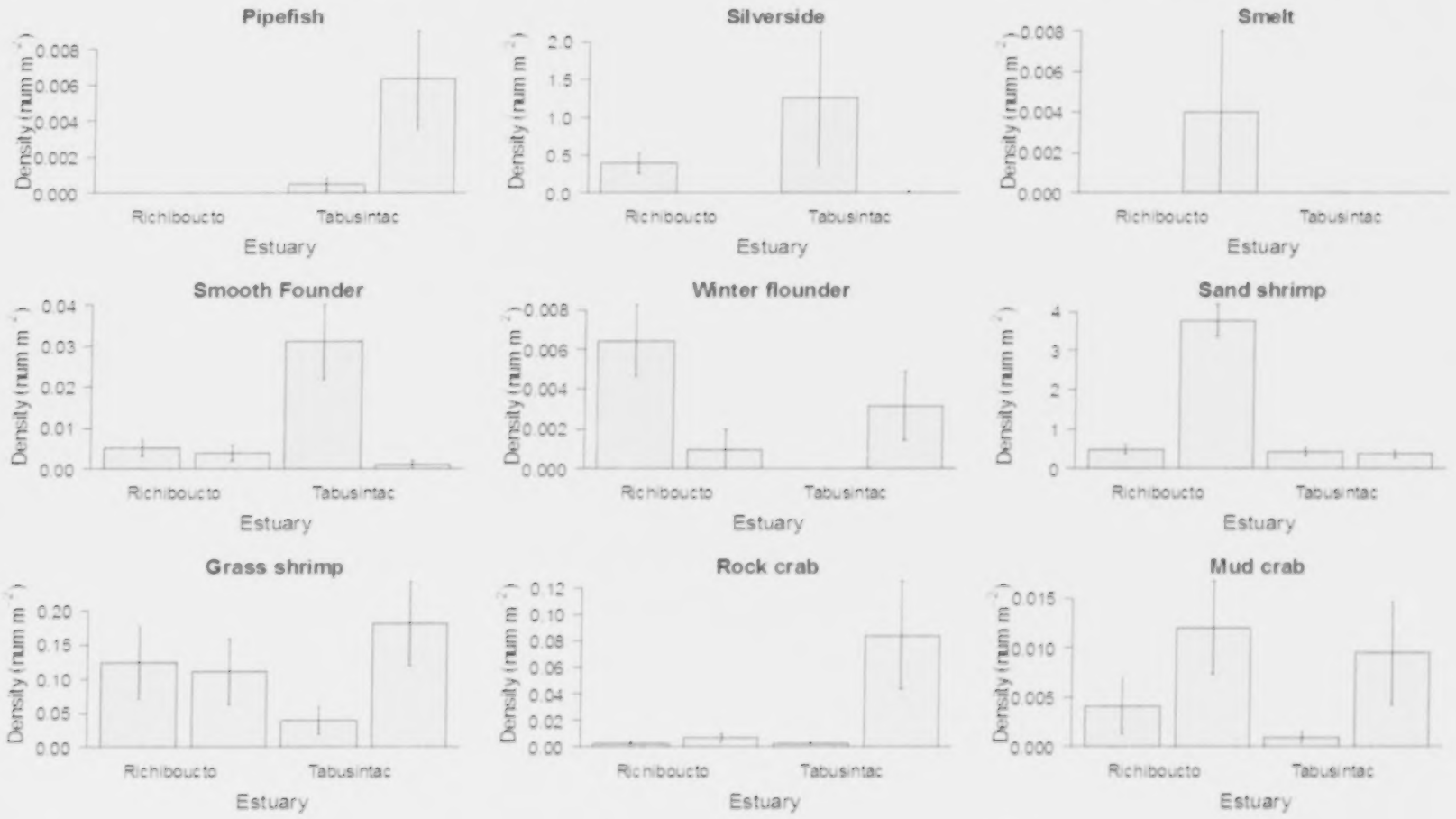

Figure 11. Comparison of species-specific density captured estimated by beach seine (green bars; CAMP) and trawl (tan bars; Skinner and Courtenay) conducted at the same sites in 2006. A subset of the species captured is shown.

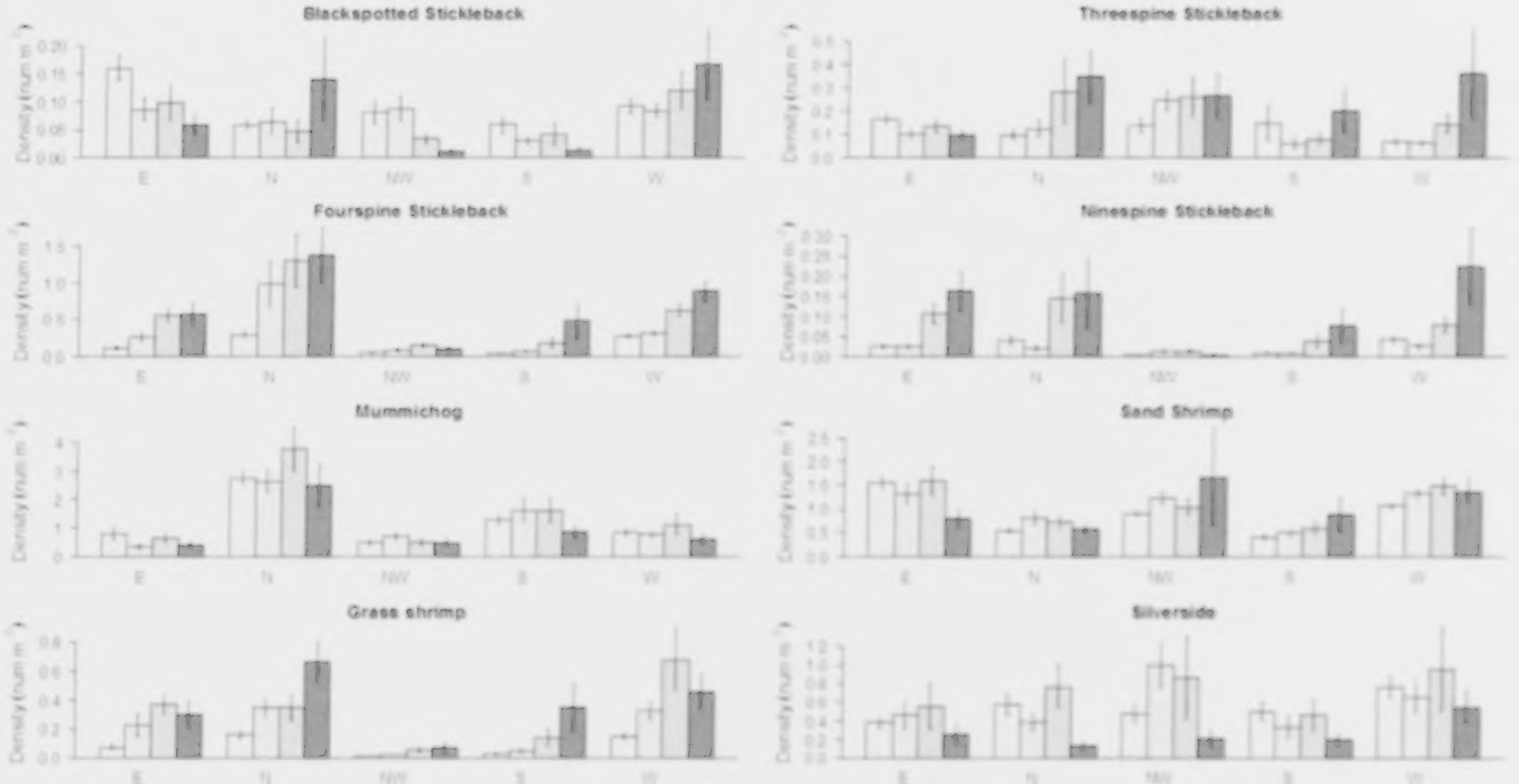

Figure 12. Species-specific density (num. m^{-2}) captured in bare habitat (tan), low, medium, or high Eelgrass shoot cover (increasing shades of green from left to right of each group of bars). Data are pooled zones of the Southern Gulf of St. Lawrence in the CAMP dataset.

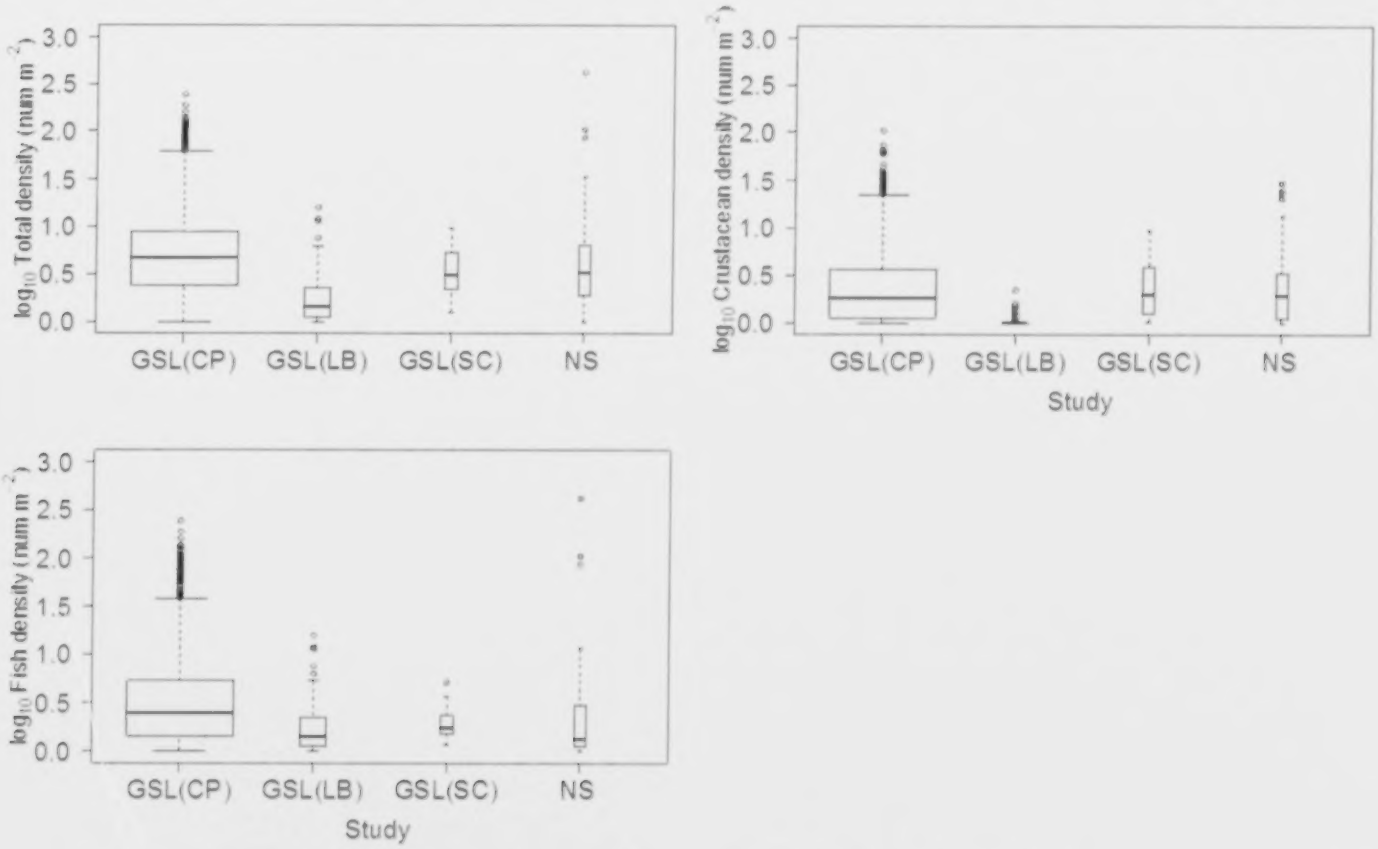

Figure 13. Density of (upper left panel) total fish community (fishes and crustaceans), (upper right panel) crustaceans, and (lower left panel) fishes across all Eelgrass field sites sampled by the different studies in Maritimes Canada. GSL = Gulf of St. Lawrence, NS = Nova Scotia, CP = CAMP, LB = Locke, Bernier and colleagues, SC = Skinner, Courtenay and colleagues. Box widths are proportional to the square root of the number of observations in each study. Data for NS are calibrated for sampling gear only and represent sizes captured. All data represent density of fish captured in the field.

APPENDICES

APPENDIX A

Table A1. Contributors of data for fish assemblages in Eelgrass beds in the Southern Gulf of St. Lawrence.

Name	Institution	Contribution
Marc Skinner and Simon Courtenay	Formally DFO Gulf Fisheries, currently Stantec (MS) and University of Waterloo (SC)	Data from NB
Andrea Locke and Renee Bernier	DFO Gulf Fisheries	Data from NB, PEI, north shore NS
Monica Boudreau, Marie-Helene Theriault, Simon Courtenay	DFO Gulf Fisheries	Data from CAMP program, NB, PEI, north shore NS

APPENDIX B

References for Table 1 in the main text.

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